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Adjudication of the Medals of the Royal Society for the year 1883, by the President and Council.

The Copley Medal to Professor Sir William Thomson, F.R.S., for (1) his discovery of the law of the universal dissipation of energy; (2) his researches and eminent services in physics, both experimental and mathematical, especially in the theory of Electricity and Thermo-dynamics.

A Royal Medal to Professor T. A. Hirst, F.R.S., for his researches in Pure Mathematics.

A Royal Medal to Professor J. S. Burdon-Sanderson, M.D., F.R.S., for the eminent services which he has rendered to physiology and pathology, especially for his investigation of the relations of Micro-organisms to disease, and for his researches on the electric phenomena of plants.

The Davy Medal to Marcellin Berthelot, For. Mem. R.S., and Professor Julius Thomsen, for their researches in Thermo-chemistry.

The Bakerian Lecture "On Radiant Matter Spectroscopy: the Detection and wide Distribution of Yttrium," was delivered by Mr. W. Crookes, F.R.S.

The Paper "On the Direct Influence of Gradual Variations of Temperature upon the Rate of Beat of the Dog's Heart," by Dr. H. Newell Martin, was appointed as the Croonian Lecture.

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XXII. *On the Ciliated Groove (Siphonoglyphe) in the Stomodæum of the Alcyonarians.*

By Sydney J. Hickson, *B.A. (Cantab.), B.Sc. (Lond.), Assistant in the Anatomical Laboratory, Oxford.*

Communicated by Professor H. N. Moseley, *F.R.S.*

Received May 23,—Read June 14, 1883.

[Plates 50, 51.]

Many years ago the distinguished naturalist Gosse (2) described two ciliated grooves in the stomach of the Sea Anemones, the function of which is to keep up the circulation of sea-water whilst the animals are retracted, and which he called the gonidial canals ("demicanaux" of Hollard (8) and "schlund-rinnen" of the German writers).

These grooves are situated on what are now known as the dorsal and ventral sides of the stomach, and their presence has been confirmed and their histology more thoroughly investigated by R. and O. Hertwig in their great work 'Die Actinien' (7).

Concerning them these authors say: "An unseren Durchschnitten durch die verschiedenen Actinienarten sind sie überall leicht zu erkennen und schienen sie sich uns durch eine besonders starke Bewimperung auszureichen."

In the genus *Cerianthus* only one groove is present (Haime) (6), and this is of great depth.

In consequence of the histological difficulties which attend the investigation of the *Alcyonarians*, their minute anatomy has not been very thoroughly investigated, and the presence of the ciliated groove on the ventral side of the stomodæum has been generally overlooked. The text-books of comparative anatomy do not mention it, nor can I find any reference to it in any memoirs except that of the Hertwigs (*l.c.*), where it is simply stated to be present on the ventral side of the stomodæum, and a rough diagrammatic sketch given of it in *Alcyonium*; and in a paper on *Sarcodictyon* by Gosse (3).

In the present communication I shall give the result of a series of investigations carried on during the last twelve months, for the purpose of tracing this ciliated grove through the various genera of *Alcyonaria*, and in referring to the various parts I shall throughout employ the following terms: I shall call the hollow communication between the mouth and the body-cavity, which is formed by an invagination of the

epiblast, the stomodæum; the portion of it that lies in the region of the mouth, the outer portion; and the portion that communicates with the body-cavity I shall call the inner portion; the general cavity of the polyps, which is sometimes short, but sometimes enormously elongated, I shall call the body-cavity; and in referring to the dimorphic forms I shall use the terms "autozooids" and "siphonozooids" which Professor MOSELEY (15) has introduced in place of the terms "polyps" and "zooids" used by Professor KÖLLIKER and others.

In *Alcyonium palmatum* the stomodæum presents in transverse section a rhombic-shaped cavity, with long lateral walls and short dorso-ventral walls; it is wide in its outer portion, but becomes considerably narrowed towards its opening into the body-cavity, so that one might describe it as a funnel which is laterally compressed (Plate 50, figs. 1 and 2).

The ciliated groove, commencing about one-third of the total depth of the stomodæum from the mouth, is continued along its ventral side as far as its opening into the body-cavity.

The stomodæum is lined by a columnar ciliated epithelium, varying in thickness from ·004 millim. to ·002 millim.

The ciliated groove is distinguished by the following peculiarities: the epithelium is thicker than it is over the rest of the stomodæum, being at least ·005 millim. thick, the free edges of the columnar epithelium cells of which it is composed are very clear and definite, and the cilia are remarkably long and strong, being from ·006 millim. to ·007 millim long.

Of the genus *Alcyonium* I have examined three other species, namely, *A. digitatum*, *A. pulmonaria*, and *A. pachyclados*, but owing to the larger number of spicules in these species, they are not so favourable for histological manipulation.

An examination of living specimens of our English *Alcyonium digitatum* revealed the fact that the cilia of the groove, moving almost simultaneously, produce a current of water from without inwards, whereas the cilia lining the rest of the stomodæum produce currents in the opposite direction. Thus a complete circulation is brought about in the polyps; the inward current produced by the cilia of the groove is probably aided by the cilia of the ventral mesenterial filaments, whilst an outward current, commencing on the dorsal and lateral mesenteries, is taken up by the action of the cilia lining the general surface of the stomodæum.

It is evident from anatomical and physical considerations that the chief part of the propulsion of these currents is performed by the cilia lining the groove on the ventral side of the stomodæum, and consequently I propose to call this groove "the siphonoglyphe."

I may summarise the characters of the siphonoglyphe in the genus *Alcyonium* as follows:—

The siphonoglyphe is present along the inner two-thirds of the ventral wall of the stomodæum (Plate 50, fig. 2), it is formed by that portion of the wall of the stomodæum

which lies between the attachment of the two ventral mesenteries only, it is marked by a distinct thickening of the epithelium, and the cilia are long and strong.

In the genus *Clavularia*, in which the non-retractile polyps stand apart from one another on a flat creeping stolon, the siphonoglyphe is marked by a considerable thickening of the wall of the stomodæum, but the cilia are comparatively short and delicate. Moreover, the siphonoglyphe does not extend over so great an area as it does in *Alcyonium*, for in a series of transverse sections no trace of it can be found in the outer two-thirds, but only in the inner third of the stomodæum.

In the genera *Spongodes* and *Nepthya* the siphonoglyphe has about the same area and extent that it has in *Alcyonium*. My specimens of *Nepthya* are not very well preserved, but, although the general histology is not easy to make out, the general features of the siphonoglyphe are quite manifest. My specimens of *Spongodes* are, however, beautifully preserved, and in them the cilia which line the general surface of the stomodæum may be easily seen. In most *Alcyonaria* which have been preserved in spirit these cilia are not easy to observe.

In the genus *Briareus* a very definite siphonoglyphe is present with long and delicate cilia.

In *Tubipora* the siphonoglyphe is well marked, and provided with a dense armature of long and strong cilia.

I was fortunate enough to obtain a fine specimen of the rare *Cœlogorgia palmosa* from Zanzibar. This genus, which resembles many of the Gorgonian Alcyonarians in the complex branching of its axis, and in the fact that the polyps are not completely retractile, differs from them in that there is no axial skeleton, but a single large canal runs along the axes of the colony and its branches. In transverse section the cavity of the stomodæum presents the appearance of a short T, the cross portion of the T being the siphonoglyphe (Plate 50, fig. 3). The siphonoglyphe is beset with cilia, which, though very much longer than those of the rest of the stomodæum, are shorter and more delicate, comparatively speaking, than those found on the siphonoglyphe of other forms.

Passing on now to those forms which exhibit the phenomenon of dimorphism.

In the genus *Sarcophyton*, the dimorphism of which was first pointed out by Kölliker (9), and subsequently confirmed by Moseley (14), the autozooids possess a siphonoglyphe which is not so well marked as it is in the preceding genera. It is only present along the inner third of the stomodæum, it never occupies a greater portion of the wall of the stomodæum than that between the two ventral mesenteries, there is no marked thickening of the epithelium of the stomodæum, and the cilia themselves are neither so numerous nor so strong as they are in other cases (Plate 50, fig. 4). In the siphonozooids, however, the siphonoglyphe is very well marked; there is a decided thickening of the epithelium; it extends along nearly the whole of the ventral side of the stomodæum, from the mouth to the body-cavity; it extends round the wall

of the stomodæum frequently as far as the insertion of the ventro-lateral mesenteries, and the cilia are characteristically long and strong (Plate 50, fig. 5).

It is exceedingly probable, from these facts, that the great part of the circulation in *Sarcophyton* is carried on by the siphonozooids, whilst the autozooids carry on the same function to a much smaller extent.

The genus *Paragorgia* is also dimorphic, a fact which seems to have been previously overlooked, and here we find a condition concerning the siphonoglyphe slightly different from that found in *Sarcophyton*.

After a careful examination of numerous autozooids, both in the retracted and expanded condition, I could find no trace of a true siphonoglyphe. There seems to be no marked thickening of the epithelium on the ventral side of the stomodæum, nor are the cilia markedly longer or stronger in that region (Plate 50, fig. 6).

In the siphonozooids, however, the siphonoglyphe is remarkably strong, and extends as far round the stomodæum as the insertion of the latero-ventral mesenteries, whilst the long cilia reach half-way across its lumen (Plate 51, fig. 8).

In *Paragorgia*, as in *Siphonogorgia*, the ova are borne by the siphonozooids, and frequently they are so full of them as to cause the stomodæum to be pushed to one side and the mesenteries to be broken (Plate 51, fig. 7).

A similar condition to this was found in the genus *Heteroxenia*. No trace of a siphonoglyphe could be seen in the autozooids, whilst a well-marked one was found in the stomodæum of the siphonozooids.

Amongst the Pennatulida I have examined two genera, *Pennatula* and *Renilla*. In the autozooids of *Pennatula* I could find no siphonoglyphe, nor in the autozooids of *Renilla*. Kölliker (9) does not mention any ciliated groove in any of the numerous Pennatulids he examined, nor does Marshall (17) in *Pennatula*, *Funiculina* and *Virgularia*. I think therefore I am justified in concluding that the siphonoglyphe does not exist in the autozooids of the Pennatulida. In the siphonozooids, however, a well-marked siphonoglyphe exists; in *Pennatula* it occupies a considerable portion of the stomodæum (Plate 51, fig. 10), and is armed with numerous long and strong cilia; in *Renilla* it is remarkable for its enormously long cilia, which stretch right across the lumen of the stomodæum (Plate 51, fig. 9).

Thus it will be seen that in the dimorphic Alcyonarians the siphonoglyphe has a tendency to disappear from the autozooids and to become very prominent in the siphonozooids. In *Sarcophyton* it still remains in the autozooids, but considerably diminished both in size and importance; in *Paragorgia*, *Heteroxenia*, and *Pennatulida* it has completely disappeared from them, whilst in all forms a well-marked siphonoglyphe is present in the siphonozooids.

In the genus *Heliopora*, some specimens of which Professor Moseley has kindly placed at my disposal, a siphonoglyphe of moderate dimensions is present.

Amongst the Gorgonidæ I have examined only two genera, *Villogorgia* and *Primnoa*, and in neither of these could I find any trace of a siphonoglyphe. In the genus

Villogorgia, although my specimens were most excellently preserved, I could find no cilia on any part of the stomodæum. I do not wish to assert for a moment that they do not exist, but if they do they must be exceedingly minute to show no trace in preserved specimens. The epithelial cells are filled with minute highly refracting particles, which conceal their outlines in exactly the same way as MARSHALL has described in the stomodæum of *Funiculina* (17, p. 14).

An interesting feature in the stomodæum of *Villogorgia* is the presence of a deep groove on the dorsal side (Plate 51, fig. 11), which is not beset, as the siphonoglyphe is, with long cilia. The epithelium of this dorsal groove is thinner than it is in other parts of the stomodæum. I have found nothing that corresponds with this dorsal groove in any other Alcyonarian.

In the genus *Primnoa*, again, I could find no trace of a siphonoglyphe, either in fully grown polyps or young buds (Plate 51, fig. 12).

Von KOCH does not describe a siphonoglyphe in any of the numerous Gorgonidæ he has examined (*Isis*, *Gorgonia*, *Sclerogorgia*, &c.), so that it seems to me probable that it does not exist in the stomodæum of Gorgonidæ, or, at any rate, in those Gorgonidæ with polyps that are not completely retractile.

It must be remembered in reference to Von KOCH's evidence that this author did not describe a ciliated groove in *Tubipora*, where it is undoubtedly present; but in this genus the stomodæum of the retracted polyps is so folded and creased that unless exceedingly thin sections are made it is easily overlooked, whereas in the non-retractile polyps of many Gorgonidæ where the stomodæum is not much folded a simple series of transverse sections would show it at once were it present.

General observations on the presence of the siphonoglyphe in the Alcyonaria.

In the three genera which have been described of simple *Alcyonaria* which do not form colonies, namely—*Monoxenia* (HÆCKEL, 5), *Hartea* (WRIGHT, 20), and *Haimea* (M. EDWARDES, 18), no siphonoglyphe has been described, and considering the small area that the circulation of these animals has to traverse, it seems to me probable that it does not exist in them. Where, however, a wider circulation was introduced, owing to the formation of complicated colonies, the aid to the circulation afforded by a siphonoglyphe became necessary.

In *Clavularia*, in which the colony consists of a number of polyps standing on a thin stolon, the circulation is not very extensive, and consequently we find that the siphonoglyphe is not very strong. In genera such as *Alcyonium*, *Spongodes*, *Nephthya*, &c., where there are long body-cavities and a considerable amount of gelatinous sarcosoma, a stronger circulation is necessary, and consequently we find that the siphonoglyphe has assumed more important proportions.

As long as the siphonoglyphe is confined to that portion of the wall of the stomodæum which lies between the two ventral mesenteries there is probably but little interference with the other functions of the stomodæum; but when the necessities of the circula-

tion require a stronger propulsive power than would be supplied by such a siphonoglyphe, certain of the polyps are arrested in their development in order that they may supply that additional power, and the colony becomes dimorphic.

The dimorphic *Alcyonaria* invariably present a considerable amount of fleshy sarcosoma, or else large spaces in which a circulation of sea-water is maintained, and it is usually the case that the circulation is entirely maintained by individuals which have become specially modified for that purpose—the siphonozooids.

Following this line of reasoning it is not difficult to understand the absence of the siphonoglyphe in the Gorgonidæ. In these animals there is always present a hard axis which may be either horny or else horny and calcareous. This axis frequently occupies the greater bulk of the colony (*e.g.*, *Primnoa*), so that the sarcosoma remains as a thin bark covering it. The result of this arrangement is that the canal system does not traverse so large an area as it does in such forms as *Paragorgia*, &c., in which there is no solid axis to the colony. The less the extent of the area supplied with canals the less the need of a strong propulsive arrangement, and consequently the siphonoglyphe is proportionately useless and disappears, the diminished circulation being carried on by the ordinary cilia of the stomodæum.

In the genus *Cælogorgia* we have an example of an Alcyonarian which resembles the Gorgonidæ in many respects, but differs from them in the important fact that a single large canal occupies the position of the solid axis of the other forms. We must suppose that there is a constant circulation going on in this axial canal as well as in the ordinary canals of the colony, and corresponding with this we find a well-marked siphonoglyphe in the polyps for carrying on this more extensive circulation.

In the genus *Solenogorgia* described by Genth (1) there is a somewhat similar condition, large canals being present in the axis of the colony and again in *Solenocaulon* described by Gray (4). A re-examination of these genera would probably reveal the fact that their polyps possess a well-marked siphonoglyphe such as we find in the genus *Cælogorgia*.

The genus *Heliopora* presents us with a condition which is not so easy to understand. The sarcosoma of the other forms of *Alcyonaria* is here represented only by a delicate layer of tissue covering the skeleton, but at the same time, owing to the large amount of space occupied by the cœnenchymal tubes, there must be a considerable amount of fluid constantly circulating throughout the colony. It is, therefore, somewhat surprising to find but a feebly-developed siphonoglyphe in the stomodæum of the polyps. It may be, however, as Professor Moseley has suggested to me, that a rapid circulation would be of no particular advantage to a colony which possesses but a small amount of living sarcosoma, or indeed by hurrying away the food particles, it might be positively disadvantageous to it. This may possibly account for the feeble siphonoglyphe.

There is however a considerable difficulty in accounting for the presence of a sipho-

noglyphe in the polyps, whilst holding the view that the cœnenchymal tubes represent siphonozooids in which the stomach, mesenteries, &c., have degenerated.

The tendency of the dimorphic forms is, as I have pointed out, to throw the siphonic function upon the siphonozooids and to eliminate it from the autozooids.

If, for any reason, it was of advantage to any dimorphic Alcyonarian to diminish the power of the circulation, this would be done by the gradual atrophy of the siphonoglyphe in the autozooids, and were this diminution insufficient the siphonozooids, or their siphonoglyphe alone, would become smaller and smaller. An example of this kind of process is presented by *Renilla*. In this genus there is but a small amount of fleshy sarcosoma, but there are large canal spaces which occupy the greater part of the colony, and here we find, owing probably to the need of only a feeble current, very small siphonozooids. In *Pennatula*, which presents a considerable quantity of sarcosoma, the siphonozooids are comparatively large.

In *Heliopora*, on the view that the cœnenchymal tubes represent siphonozooids, we should have to suppose that the siphonozooids became smaller and smaller, then completely atrophied, and subsequently a siphonoglyphe re-appeared in the autozooids. This would obviously necessitate a stage in their history in which there was no siphonoglyphe, which would be a condition very difficult to understand.

It is also difficult to believe that the mouth, stomach, and mesenteries would have all completely disappeared in this way, for even in the lowermost depths of the long body-cavities of such forms as *Tubipora*, *Alcyonium*, &c., two or more ridges remain, indicating the position of the mesenteries, and we should at least expect to find some such trace of the mesenteries in the degenerate siphonozooid.

Remarks on the classification and phylogeny of the Alcyonaria.

At present it can hardly be said that the classification of the *Alcyonaria* is in a satisfactory condition for two reasons, firstly, because no serious attempt has yet been made to trace the probable steps of the phylogeny of the group, and secondly because it is based on external zoological differences between genera rather than on the general features of their anatomy.

Taking the classification in Claus's 'Grundzuge der Zoologie' as the one most generally adopted, we find such obvious incongruities as the following: the grouping together of such colonial genera as *Alcyonium*, *Clavularia*, &c., with the simple isolated *Haimea*, *Hartea*, &c., the position of *Paragorgia* amongst the Gorgonidæ, and so on. Recently, G. von Koch (13) has suggested a classification that is based on the varieties of the skeleton, but it seems to me that the Pennatulidæ and Gorgonidæ are not so closely related as to justify their position in the same division of the same group (*Axifera*).

In presenting the following speculations on the phylogeny of the *Alcyonaria*, I am fully aware that the great difficulties of this group are only just beginning to be

appreciated, but I do so in order to point out the part which the presence or absence of a siphonoglyphe may play in the arrangement of the group, and some other points upon which the classification may turn.

There can be little doubt, I think, that the ancestral form of the *Alcyonaria* was not colonial, but was a simple isolated individual differing but slightly from the isolated genera which exist at the present day.

The fact that the three genera of isolated *Alcyonaria* are remarkably rare, present but few species, and have a wide geographical distribution (Monoxenia, coast of Arabia, Haimea, Fiji Islands, and Hartea, west coast of Ireland), point to the conclusion that they are the representatives of an ancient group which may have been much larger than it is now.

It might therefore be advisable to separate these genera as a distinct group, which might be called the PROTO-ALCYONARIA.

The next step in the phylogeny was the formation from such an isolated ancestor of a colony. The formation of the colonies may have taken place in two ways: first, by the formation of buds from the first formed polyp; and secondly, by the intermediation of a stolon upon which the young buds were formed.

A colony formed in this second way would with slight modifications give us a form such as our modern *Clavularia* or *Cornularia*.

In the genus *Tubipora* there is a stolon which I shall point out in a subsequent paper is very similar to the stolon of *Clavularia*. *Tubipora* might in fact have been derived from a *Clavularia*-like ancestor, in which the following modifications took place: The polyps became considerably elongated, and the spicules of the body-wall fused together to form a hard tubular support for them. These long polyps then became connected by canals which eventually joined together to form the horizontal platforms traversed by a network of the canals, and from them new polyps budded as they do from the original stolon.

If this reasoning is subsequently proved to be accurate it will be necessary to separate those forms with a stolon from the rest of the *Alcyonaria* into a separate group, which might be called the STOLONIFERA.

In the great majority of the *Alcyonaria* we have sufficient evidence, I think, to prove that they are formed by budding from the first-formed polyps which usually remain in the centre of the colony.

Taking a hypothetical ancestor, x, which probably had a conformation somewhat as follows: A central large polyp from which sprung, in a fan-shaped manner, a number of lateral buds of which those nearest the central polyp were the largest, we should have the rest of the *Alcyonaria* formed from it by modifications in several directions. In one direction we have the well-marked group of the *Pennatulida*. This group probably sprang from the ancestral stock at a very remote period, as is shown by the changes which have taken place in the central polyp, the arrangement of the subsequently formed polyps upon it, and the complete and universal dimorphism of

the colonies. In another direction arose the ancient group of which *Heliopora* is a survival. This group, which was formerly placed amongst the *Tabulata*, was probably very rich in genera and species in palæozoic times, but it is gradually becoming extinct.

In another direction arose the modern genus *Alcyonium* and its numerous allies. This genus differs from the ancestral form *x* chiefly in the fact that the polyps are capable of being retracted within the sarcosoma, but in other respects is probably more closely related to it than any other genera. The fact that the polyps are capable of being retracted is not one of very great importance, for we find both in this family and in the Gorgonidæ, that nearly allied genera differ from one another in this respect. The dimorphic genus, *Sarcophyton*, is probably closely related to *Alcyonium*. The presence of dimorphism is not sufficient to warrant the supposition that they sprang from different stocks, for this condition occurs in so many widely different genera that it is reasonable to suppose that it was introduced more than once in the course of the evolution of the group.

As an example of this we find that the genus *Xenia*, which probably followed another line of evolution from the hypothetical ancestor, is not dimorphic, whereas the genus *Heteroxenia*, very similar to it in other respects, is dimorphic.

The lines which evolution took in producing the large number of genera of *Primnoaceæ*, *Gorgonaceæ*, &c., are much more difficult to make out, but the following represents perhaps as near an approximate to them as our present knowledge permits.

Taking *Siphonogorgia* as a form intermediate between the ancestral type and the true Gorgonidæ, we find that the chief diversion lies in the fact that the colony has assumed an arborescent shape, and a support for it is produced by a more copious development of spicules in the axial portions of the colony. The body-cavities of the polyps, however, remain long, as they were in the ancestral form. Most probably there was another stage between *Siphonogorgia* and this ancestral form which was not dimorphic. From *Siphonogorgia*, *Paragorgia* differs chiefly in the fact that the body-cavities of the polyps have become reduced in length, and a complicated system of canals occupies the position which they formerly occupied. If *Corallium* is dimorphic, as Ridley (19) and Moseley (16) consider it to be, it was derived from an ancestor similar to *Paragorgia* in which, by a fusion of the spicules, a solid rod occupies the axis of the colony. The rare genus *Pleurocorallium* differs from *Corallium* in the fact that the polyps are not retracted into the cœnenchym, but this condition may be simply due to a more copious development of spicules in the walls of the polyps, thereby offering a physical difficulty to the retraction of the polyps.

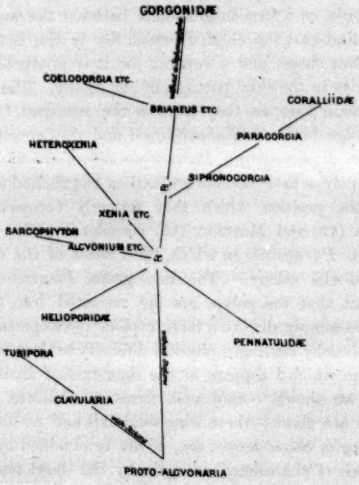
Passing by the form which I suppose at one time existed similar to *Siphonogorgia* but not dimorphic, we should obtain such forms as *Briareus*, in which the body-cavities of the polyps are short; there is no solid axis and no dimorphism, and from such genera, *Cœlogorgia*, *Solenogorgia*, &c., might be obtained by the development of large canals in the axis of the colony, or again by the development of horny or calcareous axes, we should obtain the remaining families of Gorgonaceæ, Primnoaceæ, &c.

In the Primnoaceæ I have shown that there is no siphonoglyphe, and the negative evidence of other authors affords us strong evidence for supposing that it is absent in the Gorgonaceæ. In both these families there is only a thin layer of cœnenchym covering the solid axis. If these two facts are mutually dependent upon one another, as I suppose them to be, there is sufficient reason for separating those forms which have only a thin cœnenchym covering the axis, and into which the polyps are never completely retracted, and in which there is no siphonoglyphe, into a distinct group.

This group might retain the name of the Gorgonidæ, whilst other genera which do not possess these characters and which were formerly included in the Gorgonidæ, might be placed in another group of the *Alcyonaria* altogether.

Provisionally, then, the *Alcyonaria* might be divided into the following groups :—

1. The Proto-Alcyonaria, containing the simple isolated genera.
2. The Stolonifera containing those forms with stolons such as *Tubipora*, *Clavularia*, *Sarcodictyon*, &c.
3. The Pennatulida constituted exactly as it is at present.
4. The Gorgonidæ, containing the Primnoaceæ, Gorgonaceæ, and the other families which possess no siphonoglyphe.
5. The Alcyonidæ containing all the remaining Alcyonarians.



In conclusion I should mention that my researches have been carried on in the morphological laboratory of the Oxford University Museum, and I had the great advantage of using a very valuable collection of Alcyonarians brought by Dr. GULLIVER from Zanzibar; and to the beautiful state of preservation in which I found them, many of my best results are due.

My best thanks are due to Professor LANKESTER for some excellent specimens of *Paragorgia*, *Villogorgia* and *Briareus*, and I am also deeply indebted to Professor MOSELEY, who freely placed his numerous preparations at my disposal, and whose constant aid and advice have been of invaluable assistance to me.

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Description of the Plates.

The following lettering is used throughout.

st. Stomodæum.
si. Siphonoglyphe.
siph. Siphonozooid.
aut. Autozooid.
m.f. Mesenterial filament.
sp. Spicules in the body-wall.
sp'. Spicules in the walls of the stomodæum.
sp''. Spicules in the sarcosoma.
c.c. Gastrovascular canals.
ep. Epithelium.
p. Used in figs. 11 and 12 for the spaces left after the skeletal plates have been dissolved in acid.
ov. Ova.
t. Tentacles.
v. Ventral side.
d. Dorsal side.

Fig. 1. A diagrammatic sketch of a longitudinal section through a polyp of *Alcyonium digitatum*, showing the wall of the siphonoglyphe on the ventral side with its long cilia pointing towards the body cavity, and the wall of the stomodæum on the dorsal side, which is not so thick, and beset with but small cilia. The arrows indicate the directions the currents of water take in a living polyp.

Fig. 2. Transverse section through a polyp of *Alcyonium palmatum* in the middle region of the stomodæum. The siphonoglyphe is seen on the ventral side of the stomodæum, armed with its long cilia, and in its substance are seen imbedded the long spicules.

Fig. 3. Transverse section through a polyp of *Cœlogorgia pulmosa*. The lumen of the stomodæum is seen to be T-shaped in section, the cross portion of the T forming the siphonoglyphe is armed with long, delicate cilia, and the rest of the stomodæum with short, dense cilia.

Fig. 4. Transverse section through an autozooid of *Sarcophyton pulmo* (semi-

diagrammatic). The siphonoglyphe is here feebly marked, and armed with comparatively short cilia.

Fig. 5. Section through a portion of a colony of *Sarcophyton* in a plane at right angles to the long axes of the polyps. A number of siphonozooids are seen in transverse section, separated from one another by a fleshy sarcosoma, traversed in all directions by the gastrovascular canals. The siphonoglyphe in all is seen to be well developed and situated on the same side of the stomodæum. Portions of two autozooids are seen at the sides of the drawing.

Fig. 6. Transverse section through the stomodæum of an autozooid of *Paragorgia arborea*. The stomodæum is seen to be thrown into folds, and the epithelium is armed with short cilia throughout. There is no marked thickening of the epithelium, nor lengthening of the cilia on the ventral side.

Fig. 7. Transverse section through a siphonozooid of *Paragorgia* (semi-diagrammatic). The siphonoglyphe, of very large proportions, is seen in the stomodæum. The gastrovascular canals are seen anastomosing in the sarcosoma. The spicules are omitted.

Fig. 8. Vertical section through a portion of a colony of *Paragorgia arborea*. A number of siphonozooids are seen in longitudinal section, some of which contain ova. The branching canal system is represented as it appears in section, and numerous spicules are seen imbedded in the substance of the sarcosoma.

Fig. 9. Transverse section through the stomodæum of a siphonozooid of *Renilla*. The siphonoglyphe has not a very great extent, but is armed with enormously long cilia, which extend across the lumen of the stomodæum.

Fig. 10. Transverse section through a siphonozooid of *Pennatula*. The siphonoglyphe here is of considerable size, and armed with long cilia.

Fig. 11. Transverse section through a polyp of *Villogorgia*. This drawing was kindly done for me by Mr. G. C. Bourne, of New College, Oxford, and accurately represents the appearance of one of my sections through a polyp of *Villogorgia*, which was stained in borax carmine after decalcification by means of nitric acid. The epidermic cells lining the stomodæum are not easily differentiated from one another, owing to the numerous highly refracting particles which they contain. The cilia lining the stomodæum cannot be seen with the highest power. There is no siphonoglyphe, but a deep groove (*g.*) runs down the dorsal side of the stomodæum.

Fig. 12. Transverse section through a polyp of *Primnoa lepadifera*. The stomodæum is lined by small cilia, but no siphonoglyphe is present. No trace of the dorsal groove of *Villogorgia* can be seen.

XXIII. *On the Determination of the Number of Electrostatic Units in the Electromagnetic Unit of Electricity.*

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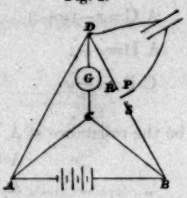
Communicated by Lord Rayleigh, *F.R.S.*

Received June 19,—Read June 21, 1883.

The values which various physicists have found for "v," the number of electrostatic units in the electromagnetic unit of electricity, differ so widely from each other that it seems important that additional experiments should be made in order to help to determine the value of this important constant. Six determinations of "v" have been published. The first determination was made by Weber, who measured the capacity of a condenser, both electrostatically and electromagnetically. Hockin and Professors Ayrton and Perry have also determined "v" in this way. Maxwell determined it by balancing the electrostatic attraction between two discs maintained at different potentials against the repulsion between electric currents circulating at the back of the discs, the currents being derived from the battery which maintained the discs at different potentials. Sir William Thomson and Mr. Shida have determined it by measuring an electromotive force both electrostatically and electromagnetically.

The following method was employed in this investigation: it is a very slight modification of the method described in § 776 of Maxwell's 'Electricity and

Fig. 1.



Magnetism.' In a Wheatstone's bridge, A B C D, with the galvanometer at G, and the battery between A and B, the circuit B D is not closed, but the points B and D are connected with two poles, R and S, of a commutator, between which a travelling piece, P, moves backwards and forwards; P is connected with one plate of a condenser, the other plate of which is connected with D. Thus when P is in contact

with S, the condenser will be charged, and until it is fully charged, electricity will flow into it from the battery; this will produce a momentary current through the various arms of the bridge. When the moving piece P is in contact with R, the two plates of the condenser are connected, and the condenser will discharge itself through D R, and as the resistance of D R is infinitesimal in comparison with the resistance of any other circuit, the discharge of the condenser will not send an appreciable amount of electricity through the galvanometer. Thus, if we make the moving piece P oscillate quickly from R to S, there will, owing to the flow of electricity to the condenser, be a succession of momentary currents through the galvanometer. The resistances are so adjusted that the deflection of the galvanometer produced by these momentary currents is balanced by the deflection due to the steady current through the galvanometer, and the resultant deflection is zero. When this is the case there is a relation between the capacity of the condenser, the number of times the condenser is charged and discharged per second, and the resistances in the various arms of the bridge.

As the investigation of this relation given in MAXWELL's 'Treatise on Electricity and Magnetism' is only an approximation, it may be worth while to give here an exact investigation of the relation between the capacity of the condenser and the resistances in the arms of the bridge; though we shall find that when the resistances have the values which they had in the present investigation, MAXWELL's formula is very nearly correct. This relation will enable us to calculate the electromagnetic measure of the capacity of the condenser.

Let $\dot{x}$ be the current in A B

$\dot{y}$,, ,, B S

$\dot{z}$,, ,, D C

then the currents in

$$\text{A C}=\dot{x}-(\dot{y}+\dot{z})$$

$$\text{A D}=\dot{y}+\dot{z}$$

$$\text{C B}=\dot{x}-\dot{y}$$

Let b be the resistance of A B

a ,, ,, A C

c ,, ,, A D

g ,, ,, D C

d ,, ,, B C

The resistances of D R, S B are so small in comparison with the other resistances that they may be neglected.

The Dissipation Function

$$=\tfrac{1}{2}\{b\dot{x}^2+a(\dot{x}-(\dot{y}+\dot{z}))^2+c(\dot{y}+\dot{z})^2+g\dot{z}^2+d(\dot{x}-\dot{y})^2\}$$

The Potential Energy

$$=\tfrac{1}{2}\frac{y^2}{C}$$

where C is the capacity of the condenser.

Thus if E be the electromotive force of the battery, we have, neglecting the self-induction of the resistance coils in the circuit,

$$\begin{aligned} b\dot{x}+a(\dot{x}-(\dot{y}+\dot{z}))+d(\dot{x}-\dot{y})&=E\\ -a\{\dot{x}-(\dot{y}+\dot{z})\}+c(\dot{y}+\dot{z})-d(\dot{x}-\dot{y})+\frac{y}{C}&=0\\ -a(\dot{x}-(\dot{y}+\dot{z}))+c(\dot{y}+\dot{z})+g\dot{z}&=0 \end{aligned}$$

or

$$\begin{aligned} (a+b+d)\dot{x}-(a+d)\dot{y}-a\dot{z}&=E\\ -(a+d)\dot{x}+(a+c+d)\dot{y}+(a+c)\dot{z}+\frac{y}{C}&=0\\ -a\dot{x}+(a+c)\dot{y}+(a+c+g)\dot{z}&=0 \end{aligned}$$

To solve these equations, assume

$$\begin{aligned} \dot{x}&=u+p\epsilon^{-\lambda t} & & \\ \dot{y}&=q\epsilon^{-\lambda t} & y&=\frac{q}{\lambda}(1-\epsilon^{-\lambda t})\\ \dot{z}&=w+r\epsilon^{-\lambda t} & & \end{aligned}$$

where t is measured from the instant when the moving piece P first touches S.

Substituting we get

$$w=\frac{aE}{(a+c+g)(a+b+d)-a^2}$$

$$u=\frac{(a+c+g)E}{(a+c+g)(a+b+d)-a^2}$$

$$\frac{q}{\lambda C}=\frac{\{(a+d)(a+c+g)-(a+c)a\}E}{(a+c+g)(a+b+d)-a^2}$$

$$r=\frac{q\{(a+b+d)(a+c)-a(a+d)\}}{a^2-(a+b+d)(a+c+g)}$$

therefore

$$\frac{r}{\lambda}=-\frac{CE\{(a+b+d)(a+c)-a(a+d)\}\{(a+d)(a+c+g)-a(a+c)\}}{\{(a+c+g)(a+b+d)-a^2\}^2}$$

But r/λ is the quantity of electricity that flows through the galvanometer whilst the condenser is being charged. If the condenser is charged and discharged n times in a second, the quantity of electricity which flows through the galvanometer in one second is nr/λ, and if this is to balance the steady current, we must have

$$n\frac{r}{\lambda}+w=0$$

or

$$nC=\frac{\{(a+c+g)(a+b+d)-a^2\}a}{\{(a+b+d)(a+c)-a(a+d)\}\{(a+d)(a+c+g)-a(a+c)\}}$$

or

$$nC=\frac{a\left\{1-\dfrac{a^2}{(a+c+g)(a+b+d)}\right\}}{cd\left\{1+\dfrac{ab}{c(a+b+d)}\right\}\left\{1+\dfrac{ag}{d(a+c+g)}\right\}}$$

Now in the actual experiment the resistances a, b, c, d, g had about the following values:—

$a=$ 1,200 B.A. units.
$b=$ 2,500 ,,
$c=$100,100 ,,
$d=$900,000 ,,
$g=$ 11,000 ,,

So that in this case the formula $nC=a/cd$ is correct to within 0·1 per cent., and it is the one we shall use to calculate the electromagnetic measure of the capacity of the condenser.

With these values of the resistances we find that λ is greater than 5000, thus the time constant of the system is very small compared with the time during which the plates of the condenser are connected together, so that the condenser is completely discharged each time.

The electrostatic measure of the capacity must be calculated from the geometrical constants of the condenser. It was necessary to use a guard ring in order to simplify the calculation, and to avoid the influence of the irregular distribution of electricity near the edges of the condenser, but as a condenser with a guard ring could not be worked by the commutator, the capacity of the guard ring condenser had to be compared experimentally with that of a condenser without a guard ring which could be worked by the commutator.

The investigation thus divides itself naturally into three parts:—

First, the theoretical calculation of the electrostatic capacity of the guard ring condenser. For this purpose it was necessary to determine the geometrical constants of the guard ring condenser.

Secondly, the comparison of the capacity of this guard ring condenser with that of a condenser without a guard ring.

Thirdly, the determination by the method just described of the electromagnetic measure of the capacity of the condenser without a guard ring.

I shall describe these parts separately.

Part I.

The calculation of the electrostatic capacity of the guard ring condenser.

The condenser, which was designed by Lord Rayleigh, is represented in section in fig. 2, and in plan in fig. 3.

Fig. 2.

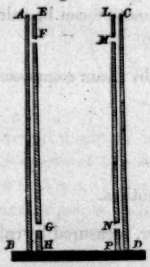


Fig. 3.

B H P D is a thick ebonite board placed in an approximately horizontal position, in this board two concentric circular grooves are cut. A cylindrical brass ring, H P, whose external diameter is about 23 centims., and whose height is about 10 centims., fits into the smaller of these grooves. Three pieces of ebonite carefully ground down to the same thickness (about 3 centims.), are placed at equal intervals on the top of this ring. On these the brass cylinder F G M N is placed; this cylinder is of exactly the same diameter as the cylindrical ring H P, and is about 60 centims. long. The cylinders, G F M N and H P, are placed so that their axes are coincident; this is tested by placing a straight-edge against the sides of the cylinder. On the top of this cylinder three pieces of ebonite are placed, and upon the top of these a cylindrical ring E L, similar to the one at the bottom; another brass cylinder, A B D C, made in three pieces, two rings similar in dimensions to the rings H P E L, and a long middle piece of the same length as the cylinder F G M N is then fitted over the other cylinders, the bottom ring fitting into the outer groove in the ebonite board; the internal diameter of this cylinder is about 25 centims. The distance between the cylinders at the top is tested by observing how far a wedge, whose vertical angle is very small, sinks down between the cylinders. When the system is properly adjusted, the variation in the distance is only a small percentage of its mean value.

The dimensions of this condenser were ascertained in the following way:—The length of the cylinder was measured by beam compasses, and the diameters of the inner and outer cylinders by callipers; the difference of these readings was not, however, taken as the distance between the cylinders, for though the error made in determining the diameter of either cylinder may be a small fraction of either diameter, yet since the diameters are nearly equal, it may not be a small fraction of their difference. The distance between the cylinders was determined by fastening the middle pieces of the two cylinders down to a flat board by a thin layer of shellac, and then filling the space between them with water which had been boiled a few hours before the experiment so as to be in a condition to absorb any air-bubbles that might be formed. The quantity of water required to fill this space was carefully weighed. This gives the volume of the water, and knowing the length of the cylinder and the diameter of one of them, the difference of the diameters can be calculated.

The results of these measurements are:—

LENGTH of cylinder, measured by beam compasses.

	60·97
	60·965
	60·97
Mean	60·968 centims.

INTERNAL diameter of outer cylinder, measured by callipers.

	9·986
	9·989
	9·992
Mean	9·989 inches, or 25·372 centims.

EXTERNAL diameter of inner cylinder, measured by callipers.

	9·254
	9·255
	9·250
Mean	9·253 inches, or 23·50 centims.

WEIGHT of water required to fill the space between the cylinders.

	4406·8 grammes at	17·5° C.
	4404·6 „	13·5°
	4401 „	12·2
	4403 „	11·5
Mean	4405·1 grammes.	

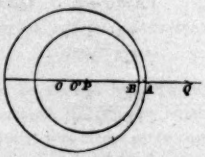
Since the greatest difference in temperature does not affect the result by one part in a thousand, the correction for temperature is neglected.

We find from these numbers that the distance between the cylinders is ·941 centim.

When the distance between the cylinders was measured by hair dividers, the least distance was found to be ·826 centim., the greatest ·984 centim., giving ·79 centim. as the distance between the axes of the cylinders.

Since the axes of the cylinders are not quite coincident, we cannot calculate the capacity by the ordinary formula. We proceed to investigate a formula which will hold in this case.

Fig. 4.



Let the figure represent a section of the cylinders by a plane perpendicular to their axes. Let O be the centre of the section of the cylinder O A, O′ the centre of the section of O′ B. Let O A$=a$, O′ B$=b$.

Let P and Q be inverse points with respect to both circles, so that

$$OP.OQ=a^2$$

$$O'P.O'Q=b^2$$

Then if $\phi=A-B\log r_1/r_2$, when r_1, r_2 are the distances of a point T from P, Q respectively, ϕ will satisfy LAPLACE'S equation and will be constant over both cylinders. Thus ϕ will be the potential of the electrical distribution, and by comparison with the ordinary form for the potential of an electrified cylinder we see that $\frac{1}{2}$ B will be the quantity of electricity per unit length upon either cylinder. Let the outer cylinder be connected with the earth so that its potential is zero, and let the potential of the inner cylinder be V.

Then we have

$$0=A-B\log\frac{PA}{QA}$$

$$V=A-B\log\frac{PB}{QB}$$

therefore

$$V=B\left\{\log\frac{PA}{QA}-\log\frac{PB}{QB}\right\}=B\log\frac{PA.QB}{QA.PB}$$

$$B=\frac{V}{\log\dfrac{PA.QB}{QA.PB}}$$

but $\frac{1}{2}$ B is the quantity of electricity per unit length upon either cylinder, and since the capacity is the quantity of electricity divided by the difference of potential, the capacity of the two cylinders

$$=\frac{1}{2}\frac{l}{\log\frac{\text{PA.QB}}{\text{QA.PB}}}$$

where l is the length of either cylinder.

Let

$$\text{OP}=x \qquad \text{OO}'=c$$

then

$$\text{OQ}=\frac{a^2}{x}. \qquad \text{PA}=a-x. \qquad \text{QA}=\frac{a^2}{x}-a.$$

therefore

$$\frac{\text{PA}}{\text{QA}}=\frac{x}{a}$$

similarly

$$\frac{\text{QB}}{\text{PB}}=\frac{b}{x-c}$$

Since $\text{O}'\text{P}.\text{O}'\text{Q}=b^2$ we have

$$(x-c)\left(\frac{a^2}{x}-c\right)=b^2$$

therefore

$$(a^2+c^2-b^2)-c\frac{a^2}{x}-cx=0$$

or

$$x^2+x\frac{b^2-(a^2+c^2)}{c}+a^2=0$$

Solving we find that

$$x=\frac{ca^2}{a^2-b^2}\left\{1+\frac{b^2c^2}{(a^2-b^2)^2}\right\}$$

approximately, supposing that as in our condenser $\frac{c^2}{a^2-b^2}$ is small.

therefore

$$x-c=\frac{cb^2}{a^2-b^2}\left\{1+\frac{a^2c^2}{(a^2-b^2)^2}\right\}$$

$$\log\frac{\text{PA.QB}}{\text{QA.PB}}=\log\frac{x.b}{a(x-c)}=\log\frac{a\left(1+\frac{b^2c^2}{(a^2-b^2)^2}\right)}{b\left(1+\frac{a^2c^2}{(a^2-b^2)^2}\right)}$$

so that the capacity of the condenser

$$=\frac{1}{2}\frac{l}{\log\left\{\frac{a\left(1+\frac{b^2c^2}{(a^2-b^2)^2}\right)}{b\left(1+\frac{a^2c^2}{(a^2-b^2)^2}\right)}\right\}}$$

$$=\frac{1}{2}.\frac{l}{\log\frac{a}{b}-\frac{c^2}{a^2-b^2}} \text{ approximately.}$$

Substituting the values of $a-b$ and b given above we find

$$\log \frac{a}{b} = \cdot 07705$$

$$\frac{c^2}{a^2-b^2} = \cdot 00027$$

and the electrostatic measure of the capacity of the condenser is consequently 396·8.

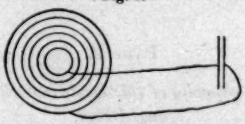
Part II.

The comparison of the capacity of this condenser with that of one without a guard ring.

As this condenser could not be worked by a commutator on account of the guard ring, it was necessary to compare its capacity with the capacity of a condenser without a guard ring. At first it was intended to compare the guard ring condenser with one of considerably greater capacity. Such a condenser was constructed, having a number of brass discs separated by thin pieces of shellac, the alternate discs being electrically connected, a weight was placed upon the disc at the top to keep the system steady; and the system was placed in a vessel formed by putting a bell-jar on a surface plate. There were two openings into this vessel, one of these was connected with a water pump; the other with the air outside the jar by a series of tubes filled with cotton wool and chloride of calcium, to free the air passing through them from dust and moisture; air was then pumped through the vessel for about 24 hours, and both openings were then closed. The capacity of this condenser was compared with that of the guard ring condenser, by connecting one plate of each condenser to earth, and the other with two points, P and Q, of a battery circuit; resistance boxes being placed between P and Q. A point O of the circuit between P and Q was then put to earth, and the resistance in the parts O P, O Q, so adjusted that when the charges of the two condensers were sent simultaneously into an electrometer there was no deflection of the needle, showing that the charges in the two condensers were then equal and opposite. In this case, the capacities of the condensers, whose plates were connected with P and Q respectively, would bear the same ratio to each other as the resistance in O Q bears to the resistance in O P. With the battery-power obtainable, this method however was found not to be sufficiently sensitive, as the resistance in either of the arms O P, O Q, could be altered by about ·75 per cent. without appreciably disturbing the equilibrium of the needle of the electrometer when the charges of the condenser were sent into it. It was therefore decided to make a condenser without a guard ring equal in capacity to the guard ring condenser, and employ the method given in § 229 of Maxwell's 'Electricity and Magnetism,' to determine when the two condensers were of equal capacity; this method can be made

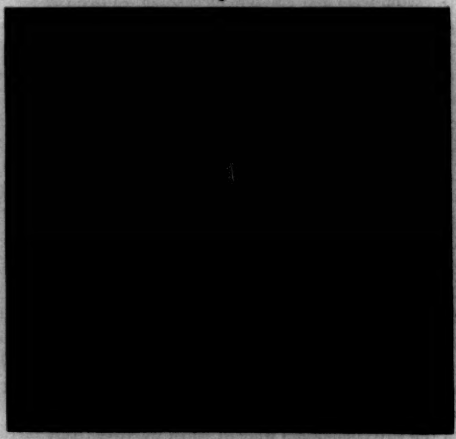
much more sensitive than the one just described, as the Leyden-jar used in MAXWELL's method can easily be raised by an electrophorus to a very high potential. The new condenser consisted of several co-axial tubes represented in section in fig. 5, The alternate tubes were connected together, and the two series connected with opposite plates of a very fine plate condenser, which was very kindly lent to me by the Rev. COUTTS TROTTER, Fellow of Trinity College.

Fig. 5.



A rough adjustment could be made by altering the number of tubes connected together, while the fine adjustment was effected by altering the distance between the plates of the plate condenser by means of a finely cut screw. The equality of this condenser and the guard ring condenser was tested by the method given in § 229 of MAXWELL's 'Electricity and Magnetism,' using a key which was very kindly lent to me by Dr. JOHN HOPKINSON, F.R.S., and which had been used by him for a similar purpose. I quote the description given of it by him in his paper on the "Electrostatic Capacity of Glass," Part II., p. 360, Phil. Trans., Part II., 1881 :—

"Fig. 3.



"Fig. 4.

"Section on line *s*, *t*, *w*.

"*a*, *c* are stiff insulated horizontal contact bars connected to the two poles of the battery. *d*, *e*, *f* are insulated springs normally touching *a* and *c* on the under side. *d* is connected by a wire to the guard ring, *e* to the plate of guard ring condenser, *f* to the sliding condenser. *b* is an insulated binding screw connected with *c* for the purpose of more conveniently introducing the battery wire. *l* is a spring connected to earth. *k* is a stiff insulated piece carrying an adjustable point *m*, normally in contact with the upper side of the insulated spring *h*. From *k* a wire leads to the quadrant of the electrometer. *k* can at any moment be put to earth by a spring key. The insulated spring *g* has its end between *e*, *f*, and *h*, and is normally in contact with neither. The springs *d*, *e*, *f* can be simultaneously bent downwards by an insulated plunger. When this plunger is struck downwards we have the following operations effected in a fraction of a second—

1°. { *d* and *e* are in contact with *a*.
{ *f* in contact with *c*.

2°. *d*, *e*, and *f* insulated.

3°. { *d* connected to *l*.
{ *e*, *f*, and *g* connected together.

4°. *e*, *f*, *g*, *h*, *k* connected together.

5°. Connexion of *k* and *h* broken.

* * * * * * * *

"The whole switch, binding screws and all, is covered with a brass cover connected to earth and provided with apertures for the connecting wires. The ebonite legs which carry the pieces *a*, *b*, *c*, *d*, *e*, *f*, *g*, *k* are attached to a brass base plate, so that if any leakage occur from *a*, *b*, *c*, *d*, *e*, or *f*, it shall be to earth and not to the electrometer."

The connexions are made in the following way. Let A denote the outer cylinder of the guard ring condenser, B the guard ring pieces, and C the inner cylinder; let A′ and C′ denote the plates of the other condenser; T the armature of the Leyden-jar, which is not connected with the earth. Then A is connected with the earth; B to A′ and to d of the key, C to e of the key, C′ to f and T to a; b and l are connected with the earth, and h is connected with the electrometer.

Before the plunger is pushed down A is put to earth; B and C to T; A′ to T; C′ to earth.

When the plunger is pushed down, before it reaches e and g, A is to earth. B and C are charged and disconnected. A′ and C′ have equal and opposite charges.

When the plunger is pushed down a little further, so that d comes into contact with l, B and A′ are put to earth, so that the charges on C and C′ are free to flow into the electrometer when the plunger goes a little further and strikes h.

If the capacities of the two condensers are equal, the charges on C and C′ are equal, and of opposite signs, and when they flow together into the electrometer, their combined effect will be zero. The distance between the plates of the plate-condenser was altered, until the needle of the electrometer was not deflected when the plunger of the key was pushed down. This method was found to be very sensitive; if after a balance had been obtained, the capacity of one condenser was altered by 1 per cent., the quantity of electricity sent to the electrometer was sufficient to drive the spot of light off the scale.

The insulation of the two condensers and the key was tested several times, both electrostatically and by attempting to pass a current through them. If either condenser was charged, and the key put in electrical connexion with it, the loss of charge in five minutes was not quite 2 per cent., so that the loss in the small time required to push the plunger down is quite negligible. When the condensers and the key were put in circuit with a battery of 150 DANIELL's elements, no current could be detected with a galvanometer whose resistance was 11,000 ohms.

PART III.

The determination of the electromagnetic measure of the capacity of the condenser without the guard ring.

This was effected by the method described at the commencement of this paper.

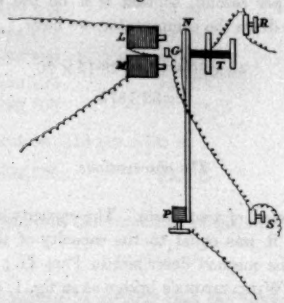
The galvanometer used had a resistance of about 11,000 ohms. It was insulated by placing it upon pieces of glass coated with paraffin.

The battery consisted of 150 DANIELL's cells, coupled up with 25 LECLANCHÉ. The DANIELL's cells were put into trays, containing 10 each. The resistance of the battery was about 2500 ohms. The insulation of the battery gave a considerable amount of trouble, but the following plan was found successful. The case containing the trays

was placed on glass supports about 2 inches thick covered with a thin layer of paraffin, while each tray was insulated from the case by pieces of ebonite.

The commutator was one which had been previously used by Lord RAYLEIGH, and had been designed by him.

Fig. 6.



The current from two GROVES' cells passes first through a tuning-fork interruptor, and then through the coils L M of an electromagnet. P N is a strip of brass with a piece of iron attached to it. When there is no current passing through the electromagnet, the elasticity of the rod P N makes it press against a screw T, which is electrically connected with a binding screw R: when the current passes through the electromagnet the magnet attracts the iron attached to the rod P N and brings it into contact with the stop G, which is electrically connected with the binding screw S. The letters P, R, S indicate the same points in this figure as in fig. 1. All the places where contact is made by the vibrating piece P N are covered with platinum, and the whole arrangement is fastened down to an ebonite board. As the current passes intermittently through the coils L N of the electromagnet, the vibrating piece P N strikes alternately against the parts G and T; when it strikes against G the opposite plates of the condenser are connected with the two poles of the battery; when it strikes against T the condenser is discharged (see fig. 1).

This commutator was found to work extremely well. When it was in good order the spot of light reflected from the mirror of the galvanometer through which the intermittent current passed never moved off one division of the scale, and the only thing by which the deflection could be distinguished from one due to a steady current was a slight indistinctness in the edge of the image of the spot of light.

The speed of the tuning-fork interruptor was found by comparing it with that of the standard fork used by Lord RAYLEIGH in his determination of the ohm in absolute measure. The standard fork vibrates about 128 times per second, while the tuning-fork used in this investigation vibrates about 32 times per second. This fork was

used to drive another of about four times its frequency, and the number of beats per second between this driven fork and Lord RAYLEIGH's standard fork was counted. At the temperature of 15° C. there were 12 beats in 20 seconds between the two forks, and the standard fork vibrated more slowly than the other. The standard fork makes 128·15 vibrations per second, so that if n be the number of vibrations per second of the fork used to drive the commutator, we have

$$4n \times 20 - 12 = 128{\cdot}15 \times 20$$
$$n = 32{\cdot}1875.$$

The observations.

The observations consisted of two parts. The capacity of the movable condenser had to be adjusted until it was equal to the capacity of the guard ring condenser. This was ascertained by the method described in Part II.; and then this adjustable condenser was put in the WHEATSTONE's bridge as in fig. 1, and the resistances of the arms of the bridge adjusted so that the deflection of the galvanometer due to the steady current was just balanced by the deflection due to the intermittent current arising from the flow of electricity to the condenser when the movable piece P was in contact with S. The resistances in the arms A D, B C (fig. 1) were kept constant, and the adjustment was effected by altering the resistance in A C.

The steady current, when it was not balanced by the current arising from the charging of the condenser, produced a deflection of the dot of light reflected from the mirror of the galvanometer of about 120 scale divisions, and as a fine wire was placed before the lamp of the galvanometer and focussed on the scale, readings could easily be made to quarter of a division.

The following are the results of the observations, and it may be worthy of remark that, as many of the pieces of apparatus used were required for the ordinary work of the laboratory, the whole arrangement had to be taken down and put together again between each determination. This must have had the effect of getting rid of a good many accidental errors, and taking it into consideration the following numbers seem as near together as could be expected for such complex observations. The resistances are given in B.A. units.

RESISTANCES in the various arms of the WHEATSTONE'S bridge, when there was no deflection of the galvanometer.

	Resistance in the arm A D.	Resistance in B C.	Resistance in A C.
1.	899,666	99,920	1294
2.	899,666	99,920	1285
3.	899,930	99,950	1297
4.	899,700	99,925	1287
5.	899,700	99,925	1297
The mean of these correct to 1/10 per cent. is			
	899,700	99,925	1292

According to Lord RAYLEIGH'S determination of the ohm the B.A. unit

$$=\cdot 987\times 10^{9}$$

so that from the formula $nC=a/cd$ we find that the electromagnetic measure of the capacity of the condenser $=\cdot 4517\times 10^{-19}$.

The electrostatic measure of the capacity of the same condenser is 396·8.

So if v be the ratio of the electrostatic unity of electricity to the electromagnetic

$$v^2=\frac{396\cdot 8\times 10^{19}}{\cdot 4517}$$

$$v=2\cdot 963\times 10^{10} \text{ in C.G.S. units.}$$

Some experiments were made with a tuning-fork vibrating 44 times a second; the results of those were found to agree very closely with those obtained when the tuning-fork vibrated 32·18 per second. The above experiments were made in the Cavendish Laboratory, Cambridge, and I have much pleasure in thanking Lord RAYLEIGH for the very valuable advice which he gave to me throughout the investigation, as well as for his kindness in designing several of the more important pieces of apparatus.

XXIV. *The Development of Renilla.*

By Edmund B. Wilson, *Ph.D., Fellow of Johns Hopkins University.*

Communicated by Professor Huxley, *F.R.S.*

Received October 5,—Read December 14, 1882.

[Plates 52–67.]

The observations recorded in the following pages were made in the course of three summers' work at the marine laboratory of the Johns Hopkins University, organised and directed by Professor W. K. Brooks, and located for the past three years at Beaufort, N.C., where the material for this paper was collected.

The abundance of *Renilla veniformis* (Cuv.), at Beaufort, suggested the desirability of a careful study of its embryology, and this was rendered still more apparent by the studies which Mr. Mitsukuri had made upon the anatomy of the adult organism.

I was therefore much pleased when a lucky accident, during the summer of 1880, put me in possession of a few very young colonies. Subsequent search over the ground resulted in the discovery of a considerable number of young colonies in various stages of growth, and I was thus enabled to make a rather full study of the growth of the colony from the simple primary or axial polyp up to the adult organism with its secondary polyps in a state of full sexual maturity. A single specimen, finally, of the ciliated larva was taken at the surface and kept in the aquarium until the free-swimming life was abandoned and the characteristic tentacles and spicules made their appearance.

An outline of the general results of these observations was published in the American Journal of Science for December, 1880, a full description being however deferred in the hope of procuring still earlier stages for a study of the embryonic development. This hope was happily realised in the following summer, when two or three lots of fertilised eggs were obtained; and, finally, in the season of 1882, the eggs were procured in considerable abundance, and a very satisfactory study of the phenomena of development was effected.

During the latter season the eggs of a Gorgonian, *Leptogorgia virgulata* (Edw. and Haime), were procured—though in small numbers only—and I have studied to some extent the development of this polyp also. The material was however scanty, and the development, so far as observed, closely similar to that of *Renilla;* hence these obser-

vations will be described only for the sake of comparison and in connexion with those relating to *Renilla*.

I have been unable to overcome entirely certain technical difficulties, and my results will therefore be found inconclusive on a few points. Furthermore, the unexpected close of the spawning period during the last season's work brought to an unwelcome close my observations on the earlier stages of development, and I have not been able, for this reason, to follow in detail the phenomena of the fertilisation of the egg and the behaviour of the segmentation-nuclei during the early stages. Still I venture to hope that my observations form a decided advance on what is now known of the development of the Alcyonaria. KOWALEVSKY's well-known observations on *Sympodium*, *Clavularia*, *Alcyonium*, and *Gorgonia* form the basis of almost the whole of our knowledge of the subject; and these observations, though of great interest, were published in a very condensed form, and were in part rendered inaccessible to many zoologists through their publication in the Russian language. They indicated that the early stages of Alcyonarian polyps would well repay more extended observation, and this expectation has perhaps been realised in the case of *Renilla*.

So far as the Pennatulacea are concerned, nothing is known of the embryonic development, and only the most meagre accounts exist concerning the mode of budding and formation of the colony. The latter phenomena however involve questions of much interest on account of the highly specialised nature of the colony as expressed in the marked polymorphism of its members and in the remarkable relations of symmetry existing between them.

For the foregoing reasons it seems to me desirable to publish these observations without further delay, since I can see in the future no near opportunity of making them complete.

Before considering the phenomena of development it will be useful to glance for a moment at some of the structural features of the adult *Renilla* and their relation to the characteristics of other Alcyonaria. For a full description the reader is referred to the well-known papers of KÖLLIKER* and EISEN,† who have described in some detail the structure of *Renilla reniformis* and *R. amethystina*.

Renilla is a genus of Pennatulacea, a group which forms the highest division of the Order Alcyonaria. The organism, when adult, is a community or colony, the members of which consist of an axial polyp and a large number of secondary polyps produced by the budding of the axial or primary individual and organically united with it. The colony has the form of a reniform disc with a deep sinus at one side into which is inserted a flexible peduncle which roots the organism in the sand. The polyps are arranged in radiating lines over the surface, projecting upwards over the general

* "Anatomisch-Systematische Beschreibung der Alcyonarien, Erste Abtheilung, Die Pennatuliden." Abdruck a. d. Abhandlungen d. Senkenb. Naturforsch. Gesellschaft, Bd. vii., viii. Frankfort, 1872.

† "Bidrag til Kännedom om *Renilla*." Kongl. Svensk. Vet. Handl., Bd. xiii.

surface but lying nearly horizontally at the margin, where new polyps continually make their appearance. Each polyp may be retracted into a "cell" which is morphologically the basal part of the polyp and forms a part of the disc.

The polyp has eight septa or mesenteries, eight pinnate tentacles, and eight mesenterial or gastric filaments, of which the dorsal pair are more slender and of different structure from the others. The two lateral pairs of septa bear the reproductive organs, male or female, as the case may be, the sexes being separate. The septa are provided with delicate longitudinal muscles by which the retraction of the polyp into its cell is effected. These muscles are always placed on the ventral sides of the septa, so that the dorsal gastric chamber contains no muscles, while the ventral chamber contains them on both sides. Thus we observe a marked bilateral symmetry in the arrangement of all the internal organs, which is further emphasized in the dorso-ventral elongation of the mouth and œsophagus. This symmetry is expressed also in the arrangement of the calyx-teeth, which are conical projections from the walls of the gastric chambers at the level of the upper face of the disc. The ventral chamber is always destitute of a tooth, the dorsal chamber always bears one, and the lateral teeth are symmetrically arranged with respect to the dorso-ventral axis.

Besides the large sexual polyps there are other forms known as the *rudimentary individuals*, or in KÖLLIKER's terminology, as the *zooids*. These are microscopic in size, have no tentacles, no mesenterial filaments, no reproductive organs, and commonly only two calyx-teeth—those, namely, on the ventro-lateral chambers. The zooids possess, in fact, only septa, mouth, and œsophagus, the latter being richly ciliated within. Two distinct forms of zooids exist. One of these is represented by a single large zooid, placed near the middle of the disc on the dorsal side, and provided with the full number of calyx-teeth. It is for the most part through the mouth of this zooid that the water is discharged which circulates through the cavities of the colony. For this reason I shall call it the *exhalent zooid*, a name which seems preferable to KÖLLIKER's term "Haupt zooid." The other zooids are arranged in groups or clusters on the dorsal sides of the polyp-cells in the median line; there are usually four such groups on each cell. It is their function to draw water from the exterior into the cavities of the colony, as may be shown by adding finely pulverised carmine to the water of the aquarium. Minute but powerful currents may thus be seen setting into the open mouths of the zooids. The zooids, like the sexual polyps, exhibit a marked bilateral symmetry in the disposition of all their organs; the mouth and œsophagus are elongated in the dorso-ventral plane, the gastric chambers are of different sizes and symmetrical arrangement, and the two calyx-teeth occupy corresponding positions on the sides of the median plane.

The colony as a whole is also bilaterally symmetrical to a very striking degree. This is more obvious in young specimens, but is always clearly marked even in the largest colonies. Each polyp has its counterpart on the opposite side of the colony, and the dorso-ventral axes of the two polyps have the same inclination to that of the

axial polyp, since the ventral chamber, which bears no calyx-teeth, is always directed outwards towards the margin of the disc. Thus the secondary polyps stand at all angles from 0° to 90° with the axial polyp; those at the sides are placed so that their dorso-ventral axes form right angles with that of the axial polyp, while those directly in front of the axial polyp coincide with it in direction.

Lastly we may note the structure of the peduncle. Its cavity is divided into a dorsal and a ventral chamber by a horizontal partition which is pierced along its sides and at its lower extremity with openings by which the chambers are put in communication. Both chambers end blindly in front, but communicate by small openings with the adjacent polyp-cells. The upper canal communicates with the exterior through the exhalent zooid already described. The horizontal partition appears to split anteriorly into a dorsal and a ventral plate, between which lies the posterior part of the body—*i.e.*, part of the cell—of the axial polyp.

The structure of the body-wall in the peduncle, where it is most fully developed, is as follows (after EISEN). Beginning with the exterior there are: (1) external epithelium; (2) a thick layer of connective tissue containing the spicules; (3) a layer of fibrous connective tissue free from spicules; (4) longitudinal muscles; (5) circular muscles; (6) internal epithelium. In other parts of the body the arrangement is somewhat different since the amount and structure of the connective tissue varies in different parts of the body and the spicules are absent from the walls of the free portions of the polyps.

Many of the structural features of *Renilla* are common to other Alcyonaria. The polyps always exhibit more or less of bilateral symmetry in the elongation of the mouth, disposition of the septa and septal muscles, grouping of the mesenterial filaments and arrangement of the reproductive organs. In all but one or two cases colonies are formed by processes of asexual multiplication, and these not uncommonly show traces of bilateral symmetry. Among the Pennatulacea bilaterality is always more or less marked, culminating in the *Renillaceæ*, where the symmetry is nearly complete.

The definite relation between the dorso-ventral axes of the secondary and primary polyps has been observed in a few other Alcyonaria, but observations on this point are very scanty. KÖLLIKER, in his great work on the Pennatulids, has described something similar among the more typical forms, and it is highly probable that further investigation would show that in all Pennatulacea definite relations of this sort exist. MOSELEY observed in *Heliopora* and *Sarcophyton** that the dorsal sides of the polyps face in a definite direction; and according to HAACKE† the polyps of *Madrepora* have a like disposition. As pointed out further on, this matter is one of much theoretical interest in connexion with the law of budding in *Renilla*.

* Phil. Trans., Vol. 166, 1876.

† "Zur Blastologie der Korallen," Jena. Zeitschrift, Bd. XIII

The polymorphism of the Pennatulids was first observed by VERRILL in 1864 in *Renilla*, and was afterwards shown by KÖLLIKER to be of general occurrence in the group. It occurs also in some of the Alcyonacea, as in *Sarcophyton* (MOSELEY) and *Heteroxenia* (KÖLLIKER), and Professor VERRILL has informed me of his discovery of rudimentary individuals in two species of *Paragorgia*, members of the Gorgonacea.

For our knowledge of the embryology of the Alcyonaria we are almost entirely indebted to KOWALEVSKY'S well-known researches, though LACAZE-DUTHIERS, many years earlier, made a few observations on the development of *Corallium*. In 1873 KOWALEVSKY gave some account of the embryological development of *Alcyonium digitatum* and *Gorgonia verrucosa*,* and in 1879 published a brief account of the early development of *Sympodium coralloides* and *Clavularia crassa*,† which he studied in conjunction with MARION. KÖLLIKER has given a brief account of the development of the buds in *Halisceptrum*, and DALYELL published fragmentary notes on the early development of *Virgularia*.‡

Even less is known in regard to the development of the colony in the Pennatulacea. FRITZ MÜLLER observed in 1864 the simple axial polyp of *Renilla* and gave a few notes upon its structure. KÖLLIKER figures a very young colony of *Pteroides* and gives a few notes concerning the young stages of *Kophobelemnon*. WILLEMÖES-SUHM has also described and figured one or two of the early stages of the colony in *Umbellularia*.§ A thorough study of the mode of budding has, however, never been made; and the observations just mentioned, though of interest, are too incomplete to be of great value.

In all of the Alcyonaria thus far studied the germ-layers appear to be differentiated through some process of delamination. Among other polyps, however—as we know from the observations of KOWALEVSKY, LACAZE-DUTHIERS, METSCHNIKOFF, JOURDAN and others—some forms undoubtedly pass through a typical invaginate gastrula stage, while others appear to develop as delaminate planulæ. BALFOUR states on the authority of KLEINENBERG,‖ that in a number of Zoantharia the segmentation is unequal, "indicating, perhaps, the occurrence of an epibolic gastrula." I shall, however, show further on, that inequality in cleavage is by no means a certain indication of epibolic invagination.

With this brief sketch of the anatomy and embryology of the Alcyonaria, in which

* "Untersuchungen über die Entwickelung der Coelenteraten, Nachrichten der Kaiserl., Gesellsch. der Freunde der Naturkenntniss der Anthropologie und Ethnographie." Moskau, 1873 (Russian). Abstract in HOFFMANN and SCHWALBE'S 'Jahresbericht,' 1875, Bd. ii.

† 'Zoologischer Anzeiger,' No. 38, 1879.

‡ 'Rare and Remarkable Animals of Scotland,' vol. ii., pp. 181–190, *t.* KÖLLIKER.

§ 'Annals and Magazine of Natural History,' vol. xv., 1875.

‖ 'Comparative Embryology,' vol. i.

only those features have been mentioned which appear of interest in connexion with the following study of *Renilla*, we may pass to a description of the observations.*

I.

SEGMENTATION OF THE EGG AND FORMATION OF THE GERMINAL LAYERS.

§ 1. *External features of segmentation.*

Renilla, like most other Alcyonaria, is dicecious, and on account of the rather marked difference in colour between the ova and spermatic capsules, the sexes may usually be distinguished by external examination. During the months of May, June, and July many *Renillas* were found with the cavities of the polyps packed with the lead-coloured ovaries or the whitish spermatic capsules. The egg or mass of sperm-cells is enclosed in a very distinct follicle of ciliated entoderm cells which is ruptured at the time of spawning, the eggs being thus discharged into the gastric cavity and thence passed out to the exterior.

The eggs make their exit through the mouths of the sexual polyps, and the time occupied in spawning is very short. They are vomited forth in great masses, together with a considerable quantity of mucus, by a reversed peristaltic movement of the œsophagus, the entire colony being usually in a state of complete expansion. The mass of eggs is often held for some time clasped in the tentacles before being thrown off into the water. All of the polyps in the central part of the disc spawn simultaneously; those near the edge of the disc often do not spawn with the others,

* It is perhaps worth while to describe briefly the methods employed in the preparation of the embryos. For sections of the early stages the most satisfactory method is that recommended by Bobretsky and so successfully employed by Mayer, Hatschek, and others. The eggs were heated in sea-water to about 60° C., and maintained at that temperature for two or three minutes in order to coagulate thoroughly the protoplasm. They were then hardened for twenty-four hours in potassium bichromate, washed two hours in sea-water, and then gradually hardened in alcohol (50 per cent. three hours, 75 per cent. three hours, 90 per cent. six hours, and then transferred to absolute alcohol). After standing twenty-four hours in picro-carmine, and again soaking a few hours in absolute alcohol, they were embedded in paraffin and vaseline and cut with the sledge microtome.

For sections of later stages the embryos were exposed for a few minutes to very dilute osmic acid ($\frac{1}{10}$ per cent., or less) until a barely perceptible brown tint was produced. After thorough washing they were transferred to weak, strong and absolute alcohol, and stained and embedded as before.

For isolation of the muscle-fibres and other elements of the tissues, the method recommended by the Hertwig brothers was employed. The larvæ were placed for ten or fifteen minutes in a mixture of equal parts of $\frac{1}{10}$ per cent. osmic acid and $\frac{1}{4}$ per cent. acetic acid in sea-water, then thoroughly washed and soaked for several days in $\frac{1}{4}$ per cent. acetic acid in sea-water. They were then stained *in toto* and teased in glycerine.

With other methods of hardening I have had no success. Bobretsky's method is highly to be recommended for the early stages, and affords very clear and satisfactory preparations.

perhaps because they are younger and less mature. The ovaries of polyps which had recently spawned were usually found to contain considerable quantities of immature eggs. Hence it seems probable that there may be several successive broods of egg in a single year, since the spawning season extends over two or three months.

It is a rather curious fact that the eggs are always laid at very nearly the same hour of the day, viz., about 6 A.M. Large numbers of *Renillas* were kept in aquaria, and the act of spawning was several times observed. In a single case only the spawning took place as early as half-past five and it was never observed to occur later than 7 A.M. This regularity appears to be independent of temperature, although this has a very important influence on the rate of development; for the hour was the same on cold and warm days. It is not unlikely that marine animals are more regular in such habits than has been suspected. A similar case is that of *Lucifer*, which, as Dr. BROOKS has observed, deposits its eggs always at the same hour, viz.: from 9 to 10 P.M.

During the discharge of the eggs by the females the males pour out the spermatic fluid in a milky cloud rising from the colony. The male element is apparently discharged, like the eggs, through the mouths of the sexual polyps. The spermatozoa are of the ordinary tailed form with pyriform heads, and swim with great activity. Fertilisation is effected in the water.

When first discharged the eggs are usually more or less distorted by pressure during their passage through the œsophagus; within a few minutes, however, they become perfectly spherical, and have an average diameter of about ·35 mm. They are of stony opacity, so that the germinal vesicle is invisible, and are destitute of any proper limiting membrane, though the peripheral layer of the vitellus is clearer and less granular than the rest. The entire substance of the vitellus is densely packed with deutoplasm granules, which upon rupture of the egg appear as clear yellowish spherules. Polar cells were never observed.

It will be convenient to describe first those changes which are visible from the exterior, leaving to the next section an account of the corresponding internal changes as discovered in sections. In a third section a review of the facts will be given, together with a discussion of their significance.

The segmentation of the egg in *Renilla* is remarkable for the surprising amount of individual variation of which it is capable. So great is this variation that it is safe to say that no two eggs ever develop in precisely the same way; and although most of the variations may be arranged in a definite series, some of them are so irregular that they seem to follow no definite law. No one indeed without actually following the entire development of some of these eggs would suppose them capable of normal development. For a long time, in fact, I passed by some of the less usual forms as due to abnormal or pathological changes, and only after repeated and careful study was able to convince myself that these peculiar embryos gave rise to active larvæ,

differing in no visible respect from those which had developed along the more usual course. The matter appeared to me of such interest and importance that I gladly availed myself of the aid of two of my fellow workers at the laboratory—Mr. H. L. Osborn and Dr. J. Meredith Wilson—in order to study as completely as possible the various forms of development. A large number of eggs, produced at different times by different individuals, were kept under continuous observation from the time of fertilisation up to an advanced stage of the segmentation; they were then proved to be capable of full and normal development by isolation in small glass vessels until the free-swimming larval stage was attained. We were thus enabled to determine with all possible certainty the fact that at least five or six well-marked modes of yolk-cleavage, with many minor variations, may occur as normal phenomena of development, that the segmentation may be at first equal or unequal, complete or partial, regular or irregular, and that a great amount of variation exists in the duration of the various stages of activity and quiescence.

The interval between fertilisation and the first cleavage varies greatly, and is in general greater when the temperature is low. Segmentation may begin within ninety minutes after fertilisation, or it may be delayed three or four hours beyond this. It was found that the longer this preliminary quiescence continued, the more apt the eggs were to pass through the less usual modes of development, while those which developed promptly were as a rule of the two common types about to be described.

1. I will first describe a common, though not the most frequent, mode of development illustrated by figs. 1 to 18. The egg having remained perfectly spherical from the time of fertilisation, becomes of irregular outline, and in two or three minutes divides into eight equal segmentation spheres. These are at first imperfectly separated (fig. 1), but soon become exceedingly distinct (fig. 2). In the individual figured the spheres swelled up slightly one minute later (fig. 3), then gradually flattened together somewhat, and the egg passed into a slightly-marked quiescent period or "resting stage" (figs. 4, 5). This continued fifteen minutes, when the spheres again swelled up, and each divided into equal parts (fig. 6) so that the embryo consisted of sixteen spheres. These again flattened together somewhat, and a second resting stage ensued (fig. 7) which continued for twenty minutes. The slight swelling of the spheres shown in fig. 3 is not accompanied by any visible cleavage. It is probably attendant upon some internal change, which may, perhaps, be a division of the nuclei —possibly of the spheres also—in a plane parallel with the surface. It is certain that such cleavages take place sooner or later, but I have not been able to trace the connexion between them and the external signs of activity (see § 2).

The segmentation now proceeded with great regularity, and appeared from the exterior to be regular and complete. Each stage of division, during which the spheres are swollen and rounded, was followed by a period of quiescence, in which the spheres were flattened and more closely pressed together. This regular alternation of rest and

activity continued for a long time, until the spheres had become very small and the embryo had begun to elongate. It is clearly shown in the series of figures from 1 to 18, of which the first fourteen are from one individual (time, 115 minutes), the last four from another specimen (time, 32 minutes). The intervals of time between the successive visible cleavages were somewhat irregular, as shown in the following statement:—

Between figures	2	and	5	9 minutes.
„	5	„	7	45 „
„	7	„	9	29 „
„	9	„	11	12 „
„	11	„	13	23 „
„	13	„	15	Not observed.
„	15	„	17	27 minutes.

In the eggs of many animals the periods follow one another with great uniformity, and the irregularity in the present case is therefore somewhat unusual. It depends perhaps on the fact that the embryo is solid, and that during the whole segmentation the cleavages take place not only in planes at right angles to the surface, but also in planes parallel to it. The latter cleavages would not be visible externally, but might retard the surface cleavages at certain periods. This is apparently the true explanation of the long delay of forty-five minutes between figs. 5 and 7; for, as we shall see in the following section, the delamination, by means of which the layers are separated, takes place at this period when the embryo consists of sixteen spheres.

2. The mode of segmentation which has been described occurred with slight variations in rather less than one-third of all the eggs studied. In the most usual case, however, the eight-sphere stage is entirely passed over, and the egg divides at once into sixteen spheres at the first cleavage.

This mode of cleavage, illustrated by figs. 30 to 37, is, except in the first stage, quite like the cleavage into eight spheres. The egg is at first perfectly spherical, then becomes irregular in form, with a wavy outline, and at length falls at once into sixteen spheres (fig. 33), which are, as a rule, of equal size. Though very distinct at first, they soon flatten together, and the egg passes into a resting stage (fig. 35), which continues for ten to twenty minutes. This quiescent period, though only slightly marked in the specimen figured, is sometimes very pronounced, so that the embryo may be nearly or quite indistinguishable from the unsegmented egg. The subsequent development is very regular, and is like the first case.

As noted above, the spheres are usually of equal size. It is, however, a common occurrence for the segmentation to be more or less unequal, as shown in figs. 38 to 44. In this case the embryo presents externally the appearance of an epibolic gastrula, consisting of macromeres and micromeres. In the eight-sphere stage, also, embryos were

sometimes observed to consist of four large spheres, capped by smaller ones, exactly as in the early stages of many epibolic gastrulas. In the sixteen-sphere stage there are often three or four larger spheres which are always placed at one pole of the egg, and are not separated by smaller spheres.

The first cleavage into eight spheres may be incomplete and irregular as well as unequal. Thus the egg shown in figs. 45 to 48 divided at first incompletely into eight (fig. 45), and then passed into a somewhat marked quiescent stage (fig. 46) of fifteen minutes' duration, one of the spheres retaining its prominence, as shown in the figure. It then divided into sixteen nearly equal spheres (figs. 47, 48), and its subsequent development was regular. A somewhat similar case is illustrated by figs. 49 to 58. In this individual the first resting stage (figs. 51, 52) was very marked, the outlines of the spheres became quite invisible, and the embryo could only be distinguished from the unsegmented egg by its slightly irregular outline. In this individual it is shown, further, that the spheres do not necessarily divide simultaneously, though this is usually the case. The sphere marked *a.* did not divide at the third general cleavage (fig. 55), but delayed until the next, or fourth, cleavage, when it divided into two spheres, *a.a.*

In these cases of slightly unequal cleavage it was in several instances observed that the smaller spheres sometimes increased considerably in size, after the cleavage was apparently complete, so as to reduce the inequality considerably. This is rendered possible, perhaps, by the circumstance to be afterwards described, that the earlier cleavages do not extend to the middle of the ovum, and the spheres are continuous at first with a central solid unsegmented mass. Or it may possibly be due to a re-arrangement of the material of the spheres, such as a change from a vertical to a horizontal elongation.

3. In the third form of segmentation to be described, of which a single case only was observed by Dr. WILSON, the egg divided at the first visible cleavage into thirty-two (±) spheres, passing over both the eight-sphere and the sixteen-sphere stages. The segmentation was somewhat unequal and became more so in later stages owing to the more rapid multiplication of the spheres at one pole. The egg developed perfectly, however, and produced a larva which appeared to be quite normal.

In the three forms of segmentation so far described, a certain number of individuals were observed to undergo considerable changes of form fifteen to twenty-five minutes before actual cleavage took place. The eggs became slightly irregular, with wavy outlines, as if about to segment; but within a few minutes they became again perfectly spherical, and remained so until the actual segmentation began. This was observed only once preliminary to the eight-sphere cleavage, and occurred in the single example of the thirty-two-sphere division. About one-fourth of those which divided at once into sixteen underwent the preliminary change.

There can be little doubt that these preliminary changes of form are attendant upon

divisions of the nuclei. The egg appears to make an effort, so to speak, at cleavage, but has not sufficient energy to complete the division of the vitellus. I shall return to this point further on. It is perhaps worth noting that the interval (fifteen to twenty-five minutes) between the preliminary change and the first cleavage is nearly always considerably greater than the ordinary resting stages (eight to eighteen minutes).

4. In a fourth form of segmentation (figs. 19 to 24), of which a single example only was observed, the egg was divided at first into two equal parts by a horizontal cleavage, and then incompletely into eight by two partial vertical furrows at right angles to each other and to the horizontal furrows (figs. 19, 20). The vertical furrows started from the horizontal one at four equi-distant points, and travelled about half-way towards the upper and lower poles. They stopped abruptly at these points however, and the egg passed into a very marked resting stage (fig. 21), during which the form was nearly spherical and the furrows could only be seen at the points of union with each other. At the next cleavage the egg divided into about sixteen spheres of different sizes (see fig. 22). The spheres remained sharply marked and rounded for twelve minutes, then flattened together slightly, but five minutes later swelled slightly and each divided into two with beautiful regularity (fig. 24). The subsequent development was regular and normal.

5. In one case an egg was observed to divide into two nearly equal parts, and then passed into a marked resting stage (figs. 25–27). In several other cases eggs were observed divided into four equal parts (figs. 28 and 29). Unluckily, the subsequent development was not followed in either case, and I cannot state whether these eggs were normal. In any case they are interesting, as filling out the series of different modes of segmentation of which the eggs are capable. In view of the great variation which certainly does exist it seems not improbable that these forms are capable of normal development.

6. In the cases so far described, the entire mass of the vitellus segments at the same time or nearly so. In several instances, however, segmentation began at one pole of the egg, leaving a large mass undivided at the opposite pole. These eggs had exactly the appearance of undergoing a partial segmentation, like that of *Pyrosoma*, or some Teleostean fishes. Thus in the egg shown by figs. 59 to 62 segmentation began with the formation of four small spheres at one pole of the egg, which then passed into a very marked resting stage. At the next cleavage (figs. 61, 62) the unsegmented portion broke up into about twelve spheres, of which two or three were somewhat larger than the others (fig. 62). The egg is now closely similar to that shown in fig. 38 which was directly derived from the unsegmented egg, and its subsequent development calls for no remark. Figs. 63 to 67 represent a similar case. In this instance the

small spheres at the second cleavage gradually extended downwards, being successively constricted off from the unsegmented mass. The first resting stage (fig. 64) was much less marked than in the individual last described, and in some individuals of this type the first period of quiescence is not attended by any flattening of the spheres, though a considerable pause always follows the formation of the first four or five small spheres.

7. Lastly, I may describe a very peculiar segmentation, shown by figs. 68 to 72. The egg when first observed consisted of three large spheres and four much smaller ones. One of the latter soon divided, and the egg passed into a slightly marked resting stage (fig. 70). At the next cleavage both large and small spheres divided (figs. 71 and 72) without apparent regularity, and the inequality still remained marked. In later stages the spheres gradually became more uniform in size, the embryo developed normally, and on the following day the free-swimming larva could not be distinguished from those produced by more usual forms of development.

Review.

The egg may divide at the first cleavage into two, four (?), eight, sixteen, or thirty-two spheres, which may be equal or unequal in size. In some cases the egg undergoes a preliminary change of form some time before cleavage, without, however, dividing, and returning afterwards to a spherical form. The cleavage into eight parts may be irregular and incomplete, and at the next cleavage sixteen spheres are formed.

Cleavage may begin at one pole of the egg with the formation of four or five small spheres, and (usually) after a quiescent period the remainder of the vitellus breaks up at once or progressively into spheres of approximately the same size as those first formed, and the egg passes into the sixteen-sphere stage.

Lastly, the segmentation may be very irregular as well as very unequal, and follows no discernible order.

I have described the various forms of segmentation in what may seem wearisome detail, since the existence of so wide a range of variation in segmentation is quite unprecedented, so far as recorded observations show. In the eggs of many animals the course of the segmentation appears to be remarkably constant, and the various cleavages follow one another with almost mathematical regularity. So far as I am aware, Brooks was the first to point out, in the case of the Oyster, in 1879, that the eggs of the same species, or even of the same individual, may normally undergo more than one mode of development. He described in the Oyster two forms of segmentation, of which one was clearly derived by an abbreviation of the other. Intermediate forms were not, however, observed, and the eggs could not be said to exhibit variation except in one definite direction. In *Renilla* the eggs vary in many directions, and the different forms of development must be due to varying structural arrangements within the egg.

This fact of extremely early variation is, I believe, one of great importance. It is evident that a structural variation in one of the segmentation spheres must make itself felt, to a greater or less extent, in the structure and development of the cells derived from it, and may therefore appear ultimately as symmetrical or correlated variations in the larva or adult organism.

Leptogorgia, like *Renilla*, is dioecious, and the eggs are fertilised in the water after their discharge from the parent. The eggs are slightly smaller (·30 millim.), and of a rosy tint, but are otherwise quite similar to those of *Renilla*. They are discharged in the same manner through the mouths of the polyps, and at the same hour of the day, viz., 6 A.M. Unlike *Renilla*, the eggs are discharged in small numbers only, each polyp producing, so far as could be ascertained, only two or three ripe eggs at a time. The polyps in all parts of the colony discharge their eggs nearly simultaneously.

The segmentation is closely similar to the most common mode of *Renilla*, but differs in some rather interesting particulars. Owing perhaps to the scarcity of material, variations in the segmentation were not observed; but only three or four eggs were kept under continuous observation from the time of fertilisation. In all these cases the egg underwent slight changes of form about an hour before the beginning of segmentation, returning afterwards to an almost perfectly spherical form. The interval between this change of form (which is undoubtedly, as in *Renilla*, the expression of an attempt at cleavage) and the beginning of actual segmentation is much greater than in *Renilla*.

At the first cleavage the egg divides into sixteen very distinct equal spheres, which soon flatten together very completely, and a strongly marked quiescent period follows, during which the embryo can scarcely be distinguished from the unsegmented egg. This continues for about twenty minutes, when the spheres again swell up and become very distinct but *do not divide*. This condition continues for several minutes when the spheres again flatten down, and a second resting stage occurs which is rather less marked than the first.

Unluckily, I did not succeed in procuring satisfactory sections of this stage, since the methods of hardening employed with *Renilla* proved useless for *Leptogorgia*. There is every reason to believe, however, reasoning from analogy, that this swelling of the spheres is accompanied by a division of their substance; and this division can only be in a plane parallel with the surface—in other words, it must be a delamination cleavage. The delamination in *Renilla*, as we shall see, takes place when the embryo consists of sixteen segmentation spheres, but with considerable irregularity, and I have not been able to connect it certainly with any external sign of activity. In *Leptogorgia* all of the spheres appear to divide at nearly the same moment, the delamination being nearly as regular as in *Gorgonia* or *Liriope*.

The egg shown in figs. 73 to 106 developed nearly in the manner just described, but with the important difference that the delamination cleavage appeared to take place when the embryo consisted of thirty-two (±) instead of sixteen spheres. When first observed the egg consisted of thirty-two (±) spheres (fig. 73), which afterwards flattened together very completely (fig. 74). Fifteen minutes later the spheres swelled up and became very prominent (fig. 75), but the embryo passed into another quiescent stage (fig. 76) without visible division of the spheres.

Hence it would seem that the period at which delamination occurs is not invariable, or it may be that it takes place at different periods in different parts of the same egg. The number of eggs observed was not large enough to determine this interesting and important point.

The remainder of the segmentation (figs. 77 to 85) is closely similar to *Renilla* and does not call for special remark. The periods of activity and quiescence alternate with great regularity, and have approximately the same duration as in *Renilla*. Although I have examined a considerable number of eggs (probably fifty or sixty), they were never found to consist of less than sixteen spheres or undergoing "partial" segmentation; and although some inequality was observed, this was never so marked as in *Renilla*. It would therefore seem that the form of segmentation is more firmly fixed than in *Renilla*.

§ 2. *Internal phenomena of segmentation.*

a. The unsegmented egg.

In the fresh state no trace of a germinal vesicle can be seen in the unsegmented egg. A series of sections shows, however, that a large vesicle is present (fig. 86) containing a very distinct germinal spot. In immature eggs the vesicle lies near the centre of the egg, but in the ripe egg it is situated near the periphery of the vitellus. It is enclosed in a delicate but very distinct membrane, and has a somewhat reniform shape with the concave side turned outwards. The interior appears to be filled with a finely granular substance, which stains intensely. No protoplasmic reticulum can be seen, and if present its meshes must be of exceeding fineness so as to produce the appearance of a fine granulation. The germinal spot is of a rounded form and lies near the centre of the germinal vesicle. It is of high refrangibility and stains intensely with picro-carmine. Under a high magnifying power it is seen to consist of a lighter clear peripheral layer, enclosing a number of spheroidal bodies, which are separated by a reticulum of deeply staining substance.

The body of the vitellus consists of a fine protoplasmic network, closely packed with rounded granules of deutoplasm, which are scarcely affected by the staining fluid. A rather narrow peripheral zone of the vitellus does not take the staining fluid, and is of a more finely granular structure than the rest of the vitellus. This zone is faintly visible in fresh eggs when flattened under the compressor, and it persists until a late

stage of the segmentation. In some preparations, however, it does not appear, and sometimes it is marked in one part of a section and invisible in other parts (see fig. 94).

As shown in fig. 86, the germinal vesicle lies in contact with this clear peripheral layer, which extends inwards slightly to meet it. In the section following that which is figured, the peripheral layer actually bends inwards so as to form a slight funnel-shaped depression leading inwards towards the germinal vesicle. Possibly this may be due to shrinkage; for I have never observed such a depression in fresh eggs. More probably it should be regarded as a kind of micropyle through which the spermatozoön enters the egg. The metamorphosis of the germinal vesicle, consequent upon fertilisation, was not followed.

As already stated, there is a considerable interval between fertilisation and the first visible cleavage. Sections through the egg show that, although the vitellus is apparently inactive, the nuclei are rapidly multiplying. The egg, which at first contains a single nucleus, becomes polynuclear and passes into the condition of a polyplast or syncytium, each nucleus corresponding to one of the future segmentation spheres, as shown by later sections.

I did not succeed in following completely the progressive multiplication of the nuclei, and can only assert that they become more numerous up to the time of cleavage, when each sphere contains a single nucleus. Many sections were obtained containing two nuclei, several with three, and a few in which four nuclei were visible. By making series of consecutive sections through the ova, it is possible to determine approximately the number of nuclei. I have thus observed the egg with four nuclei, others with four amphiasters, representing the multiplication of four nuclei into eight, and others containing eight separate nuclei. In others the number of nuclei is still greater, and in one case I was able to count sixteen nuclei, as described below. The nuclei do not always divide simultaneously, for I have, in several cases, observed eggs containing ordinary nuclei, and also typical amphiasters, with their characteristic spindles and star-shaped heads. In some cases an amphiaster and an undivided nucleus appear in the same section. In all these cases the eggs were perfectly spherical before treatment with reagents, and showed no sign of division.

Fig. 87 represents a section through a spherical unsegmented egg, a few minutes before its fellows divided into sixteen spheres. The irregularity of form is a result of shrinkage which, however, affects only the external form, leaving the substance of the vitellus uniform, and quite free from shrinkage cavities. This section is from one side of the egg, and contains two distinct amphiasters. Passing inwards, the second section contains two nuclei, and the third one. Four nuclei appear in the fourth, and four in the fifth, which is represented in fig. 88. Three of the latter are simple, while the fourth is elongated, and apparently about to become an amphiaster. Two nuclei appear in the sixth section, one in the seventh, one in the eighth, and a single amphiaster in the ninth and last. The four nuclei of sections 4 and 5 have the same

relative positions, and are doubtless identical: the nucleus of No. 3 corresponds with one of No. 2; and one of No. 6 with that of No. 7. I find, counting each amphiaster as two nuclei, the egg contains fifteen nuclei, and, counting the elongating nucleus of No. 5 as two, we have a total of sixteen nuclei, corresponding with the number of spheres formed at the first cleavage.

The segmentation nuclei bear no resemblance to the germinal vesicle or egg-nucleus. When in the quiescent state they appear as intensely stained finely granular areas, shading off, insensibly, into the surrounding mass of the vitellus, and without enclosing membrane or nucleoli. In later stages, when the vitellus has undergone division, they sometimes appear as small vesicles, containing a clear substance, and a very deeply stained nucleolus. The yolk-granules are almost always disposed in radiating lines about the nucleus, but this appearance varies greatly, and is sometimes scarcely discernible. I have no new observations to offer on the phenomena attending their multiplication, since the abundance of deutoplasm obscures the structure of the nuclei and amphiasters. Nuclei were, however, observed in every stage of division, and I will briefly describe their transformation: The nucleus becomes slightly elongated, then decidedly so, and the radiate arrangement of the surrounding granules is very marked (fig. 88). In a slightly later stage, the nucleus has a dumb-bell shape, with the vitelline granules radiating from each extremity Still later, the typical amphiaster form is attained, with two deeply stained nuclear areas, surrounded by very marked radiating lines of granules, and connected by a striated spindle. The stars then move apart, the spindle becomes attenuated. In later stages, during the cleavage process, the body of the cell splits into two at this stage on the amphiaster, the line of division passing at right angles to the spindle, near its middle point. In the unsegmented egg, the two stars simply move apart, and the spindle entirely disappears.

After the division of the amphiaster is completed, the two new nuclei assume the ordinary appearance, and the radiating arrangement of the yolk-granules becomes less marked.

The nuclei are at first situated near the centre of the egg, but as the time for cleavage approaches they travel towards the periphery, where the first segmentation spheres are to make their appearance.

b. The cleavage process.

The first division of the vitellus (fig. 89) consists in the formation of rounded prominences over its surface, of which each contains one of the nuclei derived from the continued division of the segmentation nucleus, and is therefore the equivalent of a cell (*i.e.*, a segmentation sphere). These spheres are however entirely fused together, and there is at first no trace of lines of division between them. The egg is still a polyplast or syncytium though the vitellus is being acted upon by forces which tend to split it up into separate portions corresponding in number with the nuclei. It

is important to note that whether eight or sixteen spheres are formed at the first cleavage, each contains a single nucleus only; for this shows that division of the vitellus does not always occur at the same stage in the division of the nuclei.

The prominences soon become very marked, increasing in size at the expense of the central mass and becoming at length of a pyriform shape. The egg then consists of a central unsegmented mass containing no nuclei, and surrounded by partly formed spheres, each containing a single nucleus and connected by a broad isthmus with the central mass. In some cases, at any rate, the embryo now passes into a resting stage, as shown in fig. 95. The spheres flatten together and are separated by very distinct narrow clear spaces, which terminate abruptly some distance from the centre, thus leaving the central mass quite unsegmented, and continuous with the mass of the partially-formed spheres. In the figure some of the spheres appear to be completely separated from the central mass, and this may perhaps be the case with some of them. Others however are certainly not separated from the central mass.

In the second stage of activity, or perhaps in some cases in the first, the spheres increase still further at the expense of the central mass, which becomes at length reduced to a very small remnant (fig. 92), to which the spheres are attached by narrow necks. Finally even this remnant disappears, and the completely formed spheres extend to the very centre of the embryo. A small mass of granular matter still remains in the middle of the embryo, and the spheres are attenuated at their inner ends (fig. 93). No segmentation cavity exists at this stage, but the inner ends of the cells soon become evenly rounded and a small segmentation cavity is formed (fig. 94), in which a quantity of granular *débris* usually remains. The spheres are destitute of cell-membranes, but are separated by a small quantity of intercellular substance. Their substance is completely similar to that of the unsegmented egg, the nuclei have the same appearance as in the latter, and are situated in the outer halves of the cells. The clear peripheral zone observed in the unsegmented egg is still very distinct in some specimens, but in others cannot be seen. It does not follow the lines of cleavage into the interior of the egg.

c. *Formation of the layers.*

The egg is now in the condition of a blastula in which the cells are not yet differentiated into ectoderm and entoderm. In the next change—which constitutes perhaps the most important epoch in the development of the larva—the ectoderm and entoderm are separated by a process of delamination; *i.e.*, the inner end of each sphere separates as an entoderm cell from the outer portion which remains as an ectoderm cell. A careful study of my sections taken in connexion with the external appearances, leaves no room for doubt that this is the mode in which the layers are separated; but it is clear that the cells do not in all cases perform the delamination cleavage simultaneously. On the contrary there appears to be much irregularity in this process, which is not surprising in view of the other remarkable variations in the

segmentation which have been described. Thus, in the same specimen, some of the cells may be undivided and contain simple nuclei; others contain delamination amphiasters (*i.e.*, those whose long axes are radially directed); while others have completely divided into ectodermic and entodermic moieties. Moreover, delamination cleavages may be in progress in some of the cells, while in others the cleavages are taking place in vertical planes. This is shown, for instance, in fig. 99, where two of the cells (*a*, *b*) contain delamination amphiasters, as shown by the direction of their long axes, while a third cell (*c*) is about to divide in a vertical (or radial) plane, as shown by the position of the amphiaster.

This suggests the interesting question as to whether delamination cleavages really take place in all of the cells, or may not rather be limited to the cells over a certain area. My sections are inconclusive on this point, which is of great importance in its bearing on the mode of transition between the invaginate and delaminate modes of development. (See BALFOUR'S 'Comparative Embryology,' vol. ii., p. 280, and my paper on the early stages of some polychætous annelides in 'Studies from the Biological Laboratory of the Johns Hopkins University,' vol. ii., No. 2, 1882; compare also the very interesting observations of CLAUS on "Die Entwickelung des Aequoriden-Eies," Zool. Anzeiger, No. 112, June, 1882.)

In fig. 94 one of the cells (*a*.) is in the act of cleavage, and the direction of the amphiaster and the form of the cell indicate that the cleavage is in a horizontal plane—*i.e.*, is a delamination cleavage. Fig. 96 represents a section (osmic acid) through an egg, a little later, in which the inner portions of several of the spheres are separating, or have recently separated, as entoderm cells. Unluckily, the nuclei do not appear in the section, which is furthermore somewhat disfigured by shrinkage cavities.

In a few cases I have observed at a much earlier period divisions of the nuclei, which may possibly represent delamination cleavages. Such a case is shown in fig. 98. The egg is about to divide into sixteen spheres, but contains two amphiasters, which have the same position as the true delamination amphiasters already described. It seems possible that the inner star of each amphiaster is destined to form the nucleus of an entoderm cell, and the outer star that of an ectoderm cell when division of the vitellus takes place. I have not traced this out, however, and the appearance may be open to a quite different interpretation. It is, however, certain that there is a good deal of variation in the delamination process, and the embryos do not display the beautiful regularity in this respect which has been described in some Cœlenterate eggs. As already mentioned, *Leptogorgia* appears to differ from *Renilla* in this respect, since the period of delamination is sufficiently marked to produce a special "active stage," represented externally by the simultaneous swelling of all the spheres.

At the close of the delamination process, the egg consists of a solid mass of cells in which every trace of the segmentation cavity has disappeared. As shown in figs. 99 and 100, the ectoderm does not at first form a distinct layer, the cells dovetailing with those of the central entodermic mass. As the egg passes into the resting stage,

however (fig. 97), the ectoderm becomes pretty well defined as a single layer of large cuboidal cells. The central mass is composed of large rounded polygonal entoderm cells, which differ little in structure from those of the ectoderm.

§ 3. *General considerations and comparison with other forms.*

With the formation of the germ-layers the segmentation may be regarded as finished, and it may be useful to review the facts in comparison with other forms, in order to appreciate their significance.

Examples of the continued division of the segmentation nucleus before cleavage of the vitellus are very common, but in most cases the nuclei become far more numerous before cleavage occurs than in the ovum of *Renilla*. In the case of the Isopod *Asellus* (Van Beneden) the segmentation is entirely similar to one of the forms observed in *Renilla*, the nuclei multiplying to the number of eight, and the vitellus then dividing at once into eight spheres. In view of the total dissimilarity of the adult forms, this identity in segmentation is a striking instance of the independence of the yolk-cleavage from the adult structure; and it would be clear, from this case alone, that the particular form of the segmentation may be wholly determined by secondary or adaptive causes.

This fact is rendered especially conspicuous from the astonishing amount of variation shown in the *Renilla* segmentation. This variation concerns not only small details, but also features which are usually held to be characteristic of quite different types of development. Hence we can see how readily the form of segmentation might be acted on by natural selection, for advantageous variations would certainly tend to be preserved and harmful ones destroyed. It must, however, be admitted that the action of heredity appears to have little precision in this case, for the most unlike variations appear in the eggs of the same parent, and I have not observed that any particular variation occurs more frequently in the eggs of particular individuals.

We may now inquire, What is the direct cause of the variations in the yolk-cleavage? As we have seen, the nuclei divide, so far as can be determined, in the ordinary course, and sooner or later the vitellus follows. It is highly probable that the division of the nuclei is in all cases nearly regular, and the variations of the yolk-cleavage depend upon the varying activity of the vitellus, either as a whole or in its various parts. There seems to be always a tendency to the cleavage of the vitellus simultaneously with the division of the nuclei, but this tendency varies in force or meets with varying resistance. As described above, the vitellus seems sometimes to make abortive attempts to divide simultaneously with the nuclei, these efforts being expressed in temporary changes of form in the vitellus, but not resulting in complete cleavages. In other cases the attempt is partially successful, as where the vitellus divides incompletely into eight (fig. 45). Sooner or later the tendency gathers energy enough to carry out a complete segmentation. The

egg may be able to do this at the first division of the segmentation nucleus into two, or may be unable to effect it until six successive divisions of the nuclei have taken place, and the egg therefore divides into thirty-two spheres at the first cleavage.

In searching for the cause of these variations in the activity of the vitellus, the idea at once suggests itself that it lies in the variations of the amount and distribution of the deutoplasm. It has been pretty clearly established by the researches of late years that the protoplasmic and deutoplasmic constituents of the vitellus are, in a certain sense, antagonistic to each other in their influence upon the rate of development. The protoplasm is the active part, while the deutoplasm, *as such*, is inert, and, until absorbed and converted into protoplasm, exercises a retarding influence upon development.

The egg of *Renilla* is heavily laden with deutoplasm spheres, which, as we shall see, long remain inert, and are not converted into protoplasm until a late stage of development. If we suppose—and the assumption appears fully justifiable—that the amount and distribution of the deutoplasm in the vitellus are subject to slight variation, most of the variation receives a simple explanation. It is, of course, possible, or even probable, that the activity of the protoplasm may vary also; but since the two constituents of the vitellus are, as it were, counterbalanced against each other, a variation in the amount or activity of the protoplasm must have the same effect as the opposite variation in the deutoplasm, and hence we may for the sake of simplicity consider the amount of deutoplasm alone.

The researches of Flemming, Strasburger, and others have within a few years clearly shown that the division of the nucleus of a cell produces, or is at any rate closely associated with, a tendency to division in the body of the cell. If then the deutoplasm of an egg be scanty, this tendency may be strong enough at the first division of the nucleus to overcome the inertia of the mass of the vitellus and the egg divides into two cleavage spheres at the start. This condition is permanently retained in the eggs of many animals, but in *Renilla* occurs only as a rare variation. With an increasing amount of deutoplasm, equally distributed, the cleavage of the vitellus is longer and longer delayed, though the ineffectual efforts of the vitellus may be expressed in slight changes in the form of the ovum.

Bearing these considerations in mind it is exceedingly interesting to compare the various modes of development of *Renilla* with those of other animals, and especially of certain forms existing among the Arthropods.

In *Lucifer*, as described by Brooks (Phil. Trans., 1882), the egg is transparent and nearly destitute of deutoplasm. The segmentation is regular and total, the nuclei and bodies of the spheres divide regularly and simultaneously into two, four, eight, &c., as far as the segmentation can be followed, and the spheres remain perfectly distinct from one another. In *Palæmon*, described by Bobretsky (whose Russian paper I know only from German abstracts), the deutoplasm is abundant, but the segmentation is regular and total at first. Late in the development, however, the inner ends of the high columnar cells ("yolk pyramids") fuse together to form a

homogeneous yolk. *Penæus* (Haeckel) undergoes a similar development, but the fusion of the inner ends of the spheres occurs at a far earlier stage when only four spheres are formed. Whether these are at first distinct was not determined.

In *Eupagurus* and a number of other Decapods studied by Mayer (Jenaische Zeitschrift, Bd. xi., 1877) a curious condition exists which is intermediate between the preceding forms and *Renilla*. The nucleus divides regularly into two, four, and eight, but without a concomitant cleavage of the vitellus. After the formation of the eight nuclei, however, the vitellus divides into two, four, and eight complete spheres, each of which contains one of the nuclei. In the next stage sixteen spheres are formed, but their inner ends no longer extend to the middle of the egg, the spheres having fused to form a yolk-mass as in *Penæus* or *Palæmon*. Finally in *Asellus*, already referred to, the nuclei multiply as in *Eupagurus* to the number of eight, but the vitellus then divides *at once* into eight partially-formed spheres, without undergoing the previous divisions into two and four. This condition is characteristic of about one-third of the *Renilla* eggs, but in most cases the division of the vitellus is retarded until sixteen nuclei are formed.

In rare cases cleavage is delayed until thirty-two nuclei are formed, and here again we find that this condition, though a rare variation in *Renilla*, is permanent and normal in another group of animals, namely, the Araneina (Hub. Ludwig, Zeitsch. Wiss. Zool., Bd. xxvi., 1876). In this well-known case the nuclei multiply to the number of thirty-two before the vitellus actually divides, though a partial segregation of its material is effected. From this condition the step is not great to the eggs of the Insecta and Acarina, where a still larger number of nuclei are formed before cleavage begins.

There can be no doubt that the regular division of the vitellus in geometrical progression into two, four, &c., spheres, is in general to be regarded as the most primitive mode of development, the process being only a special case of cell-division. In a number of polyps, both of the Alcyonarian and Actinarian types, as in *Clavularia*, or some species of *Actinia* (Kowalevsky), this primitive mode of development is still retained. Hence, if we regard the most frequent mode of segmentation in *Renilla*—namely, direct division into sixteen spheres—as the normal mode, the occasional division into eight, four, or two may be regarded as cases of reversion to conditions which were once the prevalent modes of development. On the other hand, the single observed case of division into thirty-two spheres shows that while the sixteen-sphere cleavage has been pretty well established, a tendency to further abbreviation still exists. We cannot doubt that if any change of condition should render a further concentration of development advantageous, this tendency or capability would come into play, and a segmentation like that of the Insecta might be produced.

As the various forms of regular cleavage may be explained as the result of variations in the amount of equally distributed deutoplasm (or in the activity of the protoplasm), so we may in part explain the various forms of unequal segmentation as due to

variations in the distribution of the deutoplasm. As shown in figs. 55–57 certain spheres may be slower in their development than others, so that their descendants are larger, a fact long since observed by ALLMAN in Hydroid eggs. This is probably caused by the presence of a larger amount of deutoplasm than common, though possibly to the tardy division of the nuclei. In the forms of "partial" segmentation shown in figs. 59–67, the large unsegmented mass must contain a number of fully formed nuclei, since it breaks up almost at once into several spheres. Hence the delay is caused, apparently, by some obstacle in the vitellus, which we may suppose to be an especially great amount of deutoplasm in one half of the egg, as is normally the case in the entodermic pole of an epibolic gastrula. It is possible in this case also to suppose that the delay is due to tardy multiplication of the nuclei, but this explanation seems less probable than the other. In some cases the small spheres are gradually constricted off from the unsegmented part, and the egg may pass into a resting stage, leaving a number of spheres only half formed (see figs. 59, 60, 63, 64). This fact strongly indicates that there is some resistance to be overcome in the vitellus, for there can be little doubt that the half-formed spheres contain fully developed nuclei.

There are a number of other facts which point in the same direction. The first formed cleavage furrows penetrate very slowly towards the centre of the ovum and, in some cases at least, do not reach the centre during the first stage of activity. The segmentation is at first, therefore, of the type which BALFOUR has termed *centrolecithal*, the egg consisting of a peripheral layer of partially-formed cells and a solid central yolk-mass. The egg differs somewhat in structure, however, from a typical centrolecithal ovum; for the central yolk-mass, so far as can be determined, does not contain at this period a greater proportion of deutoplasm than the peripheral parts, though it does so at a later stage. The failure of the cleavage furrows to reach the centre of the egg seems to be due either to the resistance being greater in the central parts, or to the exhaustion of the energy of the protoplasm before the inertia of the entire mass of deutoplasm has been overcome.

It is interesting to compare *Renilla* in this respect with *Clavularia* on the one hand and *Alcyonium* on the other, as described by KOWALEVSKY. In *Clavularia* the resistance of the entire mass of deutoplasm would seem to be less than in *Renilla*, as the egg divides completely and regularly from the first. In *Alcyonium*, on the other hand, the resistance in the central mass is greater than in *Renilla*, and the segmentation does not affect the central portions of the egg for some time. Irregular protoplasmic protuberances separate themselves from the yolk to form segmentation spheres, which after a time arrange themselves in a simple regular ectodermic layer. The central mass remains, for a considerable time, quite unsegmented, but finally breaks up into large rounded entoderm cells. Hence it appears that the cleavages do not reach the centre of the egg until the delamination takes place; and in this case the cause seems pretty clearly to lie in the greater abundance of deutoplasm in the central portion of the egg.

The principle that unequal distribution of deutoplasm produces unequal rates of

development in different parts of the egg, will not, however, account for some of the forms of unequal segmentation in *Renilla*. When, for instance, the egg divides into four larger and four smaller spheres, the former do not contain a greater number of nuclei than the latter, since at the following cleavage all are divided alike into two parts, and further, we have seen that the inequality existing at first may be considerably reduced without the occurrence of any visible cleavage. It is improbable that the cause is simply a lack of precision in the action of the vitellus, since the arrangement of the spheres is constant, so far as observed, the larger spheres being at one pole of the egg and the smaller spheres at the other. The resemblance of the egg at this stage to an epibolic gastrula has already been noted, and the idea naturally suggests itself that this resemblance may be due, not to accident, but to actual reversion of the gastrula *form*, though the essential features of the development are entirely different from those of the gastrula. There are a number of facts which indicate the derivation of the delaminate planula from an epibolic gastrula like that of *Euaxes;* and if the planula has had such an origin, it is not improbable that it might occasionally revert to the original unequal form of segmentation.

§ 4. *Changes of external form and further histological differentiation.*

At the close of segmentation the embryo is roughly spherical in form, varying considerably in outline. As development proceeds the body elongates slightly so that a longer axis (antero-posterior) can usually be made out, but the larvæ both of *Renilla* and *Leptogorgia* assume the most irregular and strange forms (figs. 100^a, 100^b, 100^c, 107). Occasionally a larva develops very regularly, preserving a nearly even oval outline until the cilia make their appearance. But in far the greater number large irregular prominences and depressions make their appearance over the whole surface of the embryo, and the form becomes so strangely modified that it is difficult to believe the shrunken and distorted larvæ capable of further development. In fact I unhesitatingly considered them at first as abnormal or dying specimens. No two of them have the same form, and they sometimes appear almost like huge *Amœbæ* with short rounded pseudopodia extended in various directions. Nevertheless the larvæ are perfectly normal, as I repeatedly proved by isolating them in small vessels and following their development. A regular oval form is once more gradually assumed (fig. 101), and most of the larvæ of twenty-four hours show no trace of the strange changes of form through which they have passed. The various prominences and processes are not capable of active movement, and the change of form is exceedingly slow. I am entirely unable to say what the significance of this curious change of form may be, and can hardly find a parallel to it in the development of other animals.

The rate of development varies exceedingly in different individuals, being sometimes twice as rapid as in other cases. In nearly all instances, however, the embryo acquires a dense and uniform covering of cilia when about twenty-four hours old, the body

having meanwhile assumed an oval form. The cilia do not at first possess the power of movement, but in a few hours become actively vibratile and propel the larva through the water. As the cilia assume their functional activity the form of the body becomes pyriform, the future oral end being the larger. This form is sometimes marked in the larva of twenty-four hours (fig. 101), but the difference between the oral and aboral extremities is usually less conspicuous than in the specimen figured.

The swimming movements become very active in the thirty-six-hours' larva, and are very characteristic. The larva swims with the aboral end directed forwards, revolving at the same time on the longitudinal axis. The larger (oral) end simply revolves about its centre while the smaller end describes a circle, so that the larva advances by a kind of cork-screw movement. Many of the larvæ swim actively about, but most of them crowd to the surface, where they arrange themselves in rows about the edge with their smaller ends turned upwards and outwards, and the swimming movements entirely cease. A very similar habit was observed by Lacaze-Duthiers in the larvæ of *Astroides*.

By the end of the third day the body becomes elongated (fig. 103), and exceedingly contractile and changeable in form. The larva may be at one moment of a worm-like elongation and at the next instant contract to a short rounded form as in fig. 105. The cilia begin to disappear and the larva swims very sluggishly near the bottom of the aquarium. During the fourth day the cilia entirely disappear and the larvæ sink to the bottom, attaching themselves loosely by means, apparently, of a mucous-like secretion. The larval life is now ended and the tentacles and spicules soon make their appearance (see § 11).

Leptogorgia agrees in the main with *Renilla*, but the development takes place more slowly. The embryo, after passing through the period of distortion, becomes of a regular oval form and acquires a uniform coating of cilia. The aboral end soon becomes slightly smaller and the larva swims with the same peculiar cork-screw movement observed in *Renilla*. The larvæ have the same habit of arranging themselves in rows at the surface of the water. On the fourth day the larvæ are much elongated (fig. 112), and possess the power of active contraction. The larval life is not ended until about the sixth or seventh day, when the cilia disappear, the larva sinks to the bottom and once more assumes a short rounded form (fig. 113), and the eight septa become faintly visible about the eighth day. Some of the larvæ attach themselves firmly by the aboral end, but others remain free as long as they were kept under observation (seven weeks). In one case two larvæ, originally quite distinct, became attached to each other near their oral ends (fig. 114). The union became very complete in a day or two, and no line of division between them could be made out. The larvæ were kept for a fortnight, but underwent very little change, and finally died. I believe their union was due simply to accidental adhesion, and has no significance bearing upon the formation of the colony. Kowalevsky observed in *Alcyonium* that numbers of the larvæ fused together in a similar manner, but their

subsequent history was not followed. It is very probable that in this case also the union was accidental and was produced by the crowding of the larvæ in small aquaria.

The formation of the septa and tentacles will be described in the following section, and we may now consider the internal histological changes which have been in progress during the stages just described.

At the close of segmentation, the embryo (fig. 97) is a solid planula consisting of a central mass of large rounded cells, enclosed by a layer of cuboidal ectoderm cells. As development proceeds, the cells of both layers continually decrease in size by multiplication, and those of the ectoderm gradually assume a marked columnar form. At the same time, the character of the cell-contents changes somewhat, the deutoplasm spheres disappearing from the ectoderm cells, which accordingly appear less coarsely granular, and remaining only in the central cells, where they continue to be very distinct, until a short time before the appearance of the digestive cavity.

The structure of an embryo of the stage superficially shown by figs. 12 and 13, is well shown in fig. 118. The section figured is from *Leptogorgia*, chosen on account of its good state of preservation; but it agrees in nearly all respects with sections through the corresponding stage of *Renilla*. The outer envelope consists of a single layer of cuboidal cells, in many of which are visible large rounded nuclei. The cells are destitute of membranes. Their contents are granular, but destitute of distinct deutoplasm spheres, and are scarcely stained by the picrocarmine. The peripheral zone of earlier stages is not visible, but in *Renilla* sections of this stage, it appears very clearly, as shown in fig. 119, taken from a somewhat later stage.

The central part of the embryo is occupied with a solid mass of large rounded entoderm cells, or, as they may for the present be called, *central* cells. The latter are enclosed by delicate but distinct membranes, which separate them sharply from each other, and from the surrounding ectoderm. Nuclei are visible in many of them; and some of the larger ones, being in course of division, contain two nuclei. The character of the cell-contents varies somewhat in different parts of the central mass. The more centrally placed cells are closely packed, with clear spherules of deutoplasm left unstained by the carmine, between which is a kind of network of finely granular, deeply stained matter. The nuclei appear as clear vesicles, surrounded by deeply stained, finely granular areas. Passing towards the outer portions of the central mass, the deutoplasm spheres become less numerous, disappearing almost entirely in the outermost cells which adjoin the ectoderm.

It is important to notice this early differentiation in the distribution of the deutoplasm; for it indicates either that the deutoplasm is more abundant here even in early stages, when no difference between the central and peripheral parts of the egg is apparent to the eye, or that the protoplasm of the outer portions is more active, and hence assimilates more rapidly the deutoplasm. Either alternative

lends support to the view suggested at p. 744, to account for the failure of the earlier cleavage furrows to reach the centre of the egg.

A comparison of figs. 118 and 97 shows that the central mass in the later stage is somewhat greater than in the earlier; and an examination of a number of sections indicates that this difference is a constant one. Hence it seems probable that more than one delamination cleavage may take place, that the central mass may from time to time receive accessions from the outer layer through the occurrence of horizontal cleavages. I have not been able to demonstrate this, though some of my sections give indications of such a process. In some cases the ectoderm cells appear elongated, and as if about to divide in the horizontal plane. It is certain, as will subsequently appear, that such cleavages occur in the ectoderm until a late period, though in later stages, when the supporting lamella is formed, the cells thus produced remain, of course, ectodermic. There seems to be no reason why such cleavages occurring at an early stage should not produce entoderm cells, and such, I am inclined to think, is actually the case.

After the stage shown in fig. 118, however, the cleavages take place for a considerable period mainly in vertical planes, so that the columnar form of the ectoderm cells becomes more and more marked.

The structure of the embryo may be far less regular than is indicated by fig. 118, since the cells often multiply more rapidly over one half of the embryo, and the division of the central cells is often irregular.

Sections through the *Renilla* embryo of about four and a half hours are represented in figs. 119 and 120. The embryo has the same general characters as in the last stage figured, but the cells have largely increased in number. The ectoderm cells have a definitely columnar form, and consist of a granular substance which is not, apparently, enclosed in cell membranes. They are separated by narrow, clear spaces which contain, apparently, a small quantity of intercellular substance. The central cells, on the other hand, are surrounded by definite membranes, which appear in the sections as narrow, dark lines.

There is still no indication of a definite membrane separating the ectoderm from the central mass. The cells of the two layers are to some extent dovetailed together, and have nearly the same structure. Here and there in the ectoderm are rounded or pyriform cells which appear to be in course of division. The clear peripheral zone still appears distinctly at the outer ends of the ectoderm cells. In some specimens it bears a fringe of fine filaments which appear like cilia, but are in reality the remnants of the spermatozoa with which the embryo remains covered for a considerable period.

In the embryo of eight hours (figs. 122–124) the ectoderm layer is sharply differentiated from the central mass, but the latter has undergone very slight change except in the further division of its cells. The ectoderm cells have now a high columnar form, though here and there rounded cells may be observed (fig. 122). At their inner ends, where they are usually somewhat expanded, they abut against the

cells of the central mass, and in many parts of the sections are separated from the latter by an irregular, scarcely defined membrane (this is represented as too distinct in the figures). In some sections the membrane does not appear. This membrane appears to be the first rudiment of the supporting lamella ("Stützlamella") which is so characteristic a structure among the polyps and hydroids, but the main body of the lamella is formed somewhat later, as described in the next section. The ectoderm cells now stain very differently from those of the central mass, and the peripheral zone has disappeared. The substance of the cells appears scarcely coloured, while the nuclei are deeply stained. The central cells, on the other hand, stain deeply, so as to be very sharply differentiated from the ectoderm in colour as well as in form. The deutoplasm spheres have the same distribution as in earlier stages, being very abundant and clearly defined in the more centrally placed cells (fig. 124) and becoming indistinct and scanty, or quite disappearing in the outer cells. There is still not the least trace of a digestive cavity.

I am unable to say what the significance of the peripheral zone may be. A very similar zone is described by Hoffmann in the ectoderm cells of *Tetrastemma* at an early stage and by Rabl in the ectoderm of *Unio*. It is possibly concerned in the formation of the cilia, but this seems improbable, since it disappears in *Renilla* long before the cilia are formed.

In this stage the sections of the embryo sometimes appear exactly as if taken from an epibolic gastrula, for the ectoderm cells may be very different both in size and form on opposite sides of the embryo. This appearance is however entirely deceptive, and is produced simply by the tardy multiplication of the cells over one half of the embryo.

§ 5. *Formation of the entoderm and appearance of the digestive cavity.*

The embryo has thus far remained quite solid with no trace of a digestive cavity. For some hours longer this condition continues, the only change consisting in the multiplication of the cells of both layers. About the twentieth hour, however, or at the time when the cilia make their first appearance, peculiar changes become evident in the central cells which are the forerunner of the formation of the proper entoderm and the stomach cavity. The deutoplasm spheres disappear completely from the central cells, which then have a coarsely and irregularly granular appearance with very distinct membranes and deeply stained nuclei. The central mass is still solid, however, and the cells are all of the same irregularly rounded form. In a few hours a very perceptible difference can be seen between the outer and the inner cells of the central mass. Those which lie just beneath the ectoderm (figs. 125 and 126, *en.*) become much clearer, their substance stains very little, and many of them assume a slightly columnar form. Their nuclei are very distinct, of a slightly oval form, and very deeply stained. The cells are in some parts of the larva arranged in a single layer,

but in other parts seem to be placed two or more deep. It is difficult in this, as in subsequent stages, to say whether this appearance of several layers in the entoderm may not be due to the sections being always more or less oblique in different parts of the section; but I believe, after examination, that they do form several layers in some parts of the embryo at this stage. This layer of clear cells is the permanent or true entoderm.

The central cells, on the other hand, remain rounded and very granular, and stain more deeply than the entoderm cells. They become ultimately disorganised and are absorbed as food by the true entoderm cells; hence they may hereafter conveniently be termed the *yolk-cells*.

The yolk-cells form at first a solid mass which is directly continuous with the entoderm cells surrounding it. Soon, however (fig. 125), the yolk-cells become more loosely connected, and considerable cavities appear in the central mass in which the yolk-cells often lie quite disconnected from the other cells or united in groups of two or more cells. It is difficult to gain a clear idea of the changes which bring about this condition. Apparently the entire larva increases somewhat in size while the membranes of the yolk-cells become partially disorganised. In parts of the yolk-mass the cell-contents with their nuclei seem actually to drop out of the cell-membranes, which remain as a delicate network (fig. 126) in which the form of the cells is still perfectly preserved. Possibly this occurs only as a result of rough handling after the sections are made. Still I believe it may be in part a normal occurrence and that some at least of the free naked cells in the yolk-cavities may have been thus liberated. Others of the free cells have at first delicate cell-membranes, but these afterwards disappear.

The yolk-cells are rounded, but vary greatly in form and size. Most of them are still distinctly nucleated, but the nuclei are less sharply defined and have less regular outlines than those of the entoderm cells. The cell-substance contains no deutoplasm spheres, and consists of a granular substance which stains irregularly and in some places not at all. Besides the yolk-cells there is a considerable quantity of granular substance in the form of small balls or masses lying in the yolk-cavities, and here and there may be seen a deeply stained free nucleus surrounded by a small quantity of granular matter. It is probable that the granular matter is derived from the breaking down of the yolk-cells, but it is difficult to say how far these appearances are the result of normal phenomena of disintegration, and how far due simply to mechanical injuries produced by manipulation. The general features of a section of this stage (twenty-two and a half hours) are well shown in fig. 125.

Still later the yolk-mass becomes completely disorganised, breaking up into a kind of *débris* in which several distinct elements can be recognised (fig. 127). There are: firstly, rounded cells with distinct nuclei and membranes, which are simply free yolk-cells; second, similar but usually smaller cells which have no membrane; third, free nuclei which are usually associated with a small quantity of granular matter; fourth,

small rounded granular bodies, about one-fourth the size of the yolk-cells and destitute of nuclei; and fifth, still smaller granules, apparently produced by the disintegration of the preceding.

The entoderm (*en.*) has now a very different appearance from that of the last stage. The cells are columnar, with very distinct oval nuclei, which are always situated in the outer half of the cells; but the cell-contents are dark and opaque, being densely packed with granules. The cell-outlines are thus more or less obscured, and though always distinct towards the outer part of the cell may be quite invisible towards the base. The granulation is of quite different appearance in the inner and outer parts of the cells. In the basal (*i.e.*, outer) part the granules are fine and closely packed, and are left nearly or quite unstained, while in the inner ends of the cells the granulation is coarse and irregular, and stains more readily. This difference is so constant that in most specimens the basal granulation forms a pretty distinct narrow zone extending around the entire entoderm. The cells are in some parts of the sections only one layer deep, but in other parts the entoderm consists of several layers and varies greatly in thickness.

The general features of a twenty-nine-hours' larva are shown in fig. 128, and a portion of the body-wall, more highly magnified, in fig. 129. The body is now distinctly elongated and the oral end can be distinguished by its greater size. The entoderm is composed of high columnar cells, and is everywhere much thicker than the ectoderm. The gastric cavity is clearly defined and the yolk-mass is greatly reduced in bulk. Under a high power (fig. 129) the yolk-cells are found to have nearly disappeared, though here and there one may still be recognised. The yolk is almost entirely composed of the naked granular spheroidal bodies described in the last stage. They vary a good deal in size, but are on the average rather larger than the nuclei of the entoderm cells. They appear to have had their origin in the breaking up of the yolk-cells, though some of them are perhaps small yolk-cells which have lost their nuclei.

The entoderm cells (*en.*) are much elongated and present some interesting characters. Towards their bases they are filled as before with fine granules, which stain very slightly, and are arranged in a distinct zone encircling the entire larva. Their inner portions (apical) present a confused coarsely granular appearance, entirely unlike that of the basal granulation. The cells seem to contain rounded granular masses, which have the same appearance as the smaller spheroidal bodies of the yolk, which lie outside the cells in the stomach cavity. As in the last stage, the granules are so abundant that it is difficult to make out the outlines of the cells, which only appear clear and well defined at their inner ends.

The yolk gradually disappears as development progresses and the larva rapidly increases in size. Much variation exists in the length of time required for absorption, but it is always complete, so far as I have observed, by the forty-eighth hour, and the gastric cavity is left empty, or sometimes containing a small quantity of a delicate *débris*, which appears to be the remains of the membranes of the yolk-cells. After

the yolk is completely absorbed the contents of the entoderm cells again change their character, as shown in fig. 130 (fifty-two hours). They become once more clear, and the basal granulation nearly disappears. The cells still contain a considerable quantity of granules, but the contrast with the preceding stages is marked. The cell-outlines consequently become much more distinct. The nuclei are deeply stained, very conspicuous, and are situated always in the inner parts of the cells.

Conclusions.

Although I have made many sections of larvæ prepared by various methods while yolk-absorption was in progress, I have failed to obtain decisive evidence as to the precise *modus operandi* by which the yolk-cells or their remains are absorbed by the entoderm cells. This failure is due to the excessive minuteness and delicacy of the tissues which renders it extremely difficult to make satisfactory preparations of them. But a careful study of the sections inclines me to the belief that the smaller particles of the yolk-*débris* are engulphed bodily by the entoderm cells Amœba-fashion, the process of digestion being completed within the body of the cell: that, in other words, the young *Renilla* is nourished by a form of intra-cellular digestion. As we have seen, the cells are at first clear and nearly destitute of granules. They become granular, however, and increase in size as soon as the disintegration of the yolk-cells begins, and their granular appearance continues until the absorption of the yolk is completed, when they become again clearer. The large, coarse granules in their inner ends (*i.e.*, those turned towards the yolk-mass) have the same appearance as the small yolk-granules lying just outside the cells, and the entoderm often contain rounded granular masses which are very similar, though with less distinct outlines, to the yolk-spheroids of the digestive cavity. The spheroids may often be observed to lie directly upon the entoderm cells, and the inner ends of the latter are sometimes produced into small amœboid processes reaching out into the digestive cavity, though this is rare.

These appearances suggest, though they do not prove, that the yolk-granules and spheroids pass bodily into the cells. I have never seen them in the act of passing into the cells, but the technical difficulties are great, and the other considerations seem of sufficient weight to warrant the provisional acceptance of the view advanced above.

This conclusion, if well-founded, is of interest in connexion with recent discoveries in regard to intra-cellular digestion in Cœlenterata and Turbellaria. The occurrence of such a form of digestion in the sponges has long been a familiar fact, and the more recent researches of Metschnikoff, Claus, Gegenbaur, Parker and Ray Lankester have shown that an essentially similar mode of digestion occurs in the adults of many Cœlenterata belonging to the higher groups, namely: in *Hydra*, Hydroid polyps, Hydromedusæ, Acalephs, Actiniæ, Ctenophora and Siphonophora. Metschnikoff showed in 1878 that the same remarkable process takes place in a number of fresh water Turbellaria, and he has ascribed to it an important phylogenetic significance. He

points out the fact that intra-cellular or amœboid digestion is confined, so far as known, to the most primitive groups of the Metazoa and in the Cœtenterates seems to be the normal and most frequent if not the only process. The digestive functions of an entoderm cell in these cases are identical with those of a unicellular Protozoa, and METSCHNIKOFF is inclined to consider the former as an actual survival of the latter—a physiological character which was originally present in all Metazoa then existing, and has only been lost in higher forms. LANKESTER even suggests that the absorption of unsaponified fats in the highest Metazoa may possibly be a last relic of the primitive mode of digestion.

None of the writers on this subject have pointed out the identity of the process with that of the absorption of the yolk in *Astacus*, described by REICHENBACH in 1877 (Zeitschrift für Wiss. Zool., Bd. xxix., 1877). In this case the amœba-like action of the entoderm cells was observed with the greatest clearness. The cells put forth large pseudopodia, and actively engulph the yolk-granules which were observed in every stage of the passage from the yolk-mass into the cell-bodies. The ingestion takes place, it is true, at the basal instead of the apical end of the cells, since the yolk lies outside the archenteron; but this circumstance does not tell against the identity of the process with that of adult Cœlenterata and Turbellaria and of the larval *Renilla*. WOLFSON has observed a similar process in the yolk-absorption of *Lymnæus*, and in this case the nutriment, as in *Renilla*, is contained within the archenteron (see Bulletin de l'Académie Impériale des Sciences de Saint-Pétersbourg, tom. xxvi., pp. 79–99, 1880. Lu le 9 Octobre, 1879).

It is interesting to find the embryonic entoderm cells exhibiting this primitive mode of digestion, though it is clearly to be regarded simply as an adaptation connected with the presence of a large amount of food-yolk. Still the idea is suggested that the amœba-like ingestion of food in the larva may perhaps be due to a kind of reversion, the reappearance in the larva of a feature which, in the case of *Astacus* and *Lymnæus* at least, has become quite dormant in the adult. Whether it exists in the adult *Renilla* I have been unable to determine, but it cannot be observed in the young transparent colonies (see p. 786).

Whatever be the mode of absorption, the granular basal zone, so often referred to, appears to be a reserve store of food-material—either the actual remains of the ingested food-granules, or a new store of granules laid up for future use by the protoplasm after being richly fed. It would seem that the cell packs away its reserve supply of food in its basal part, leaving the apical or inner end free to continue the active work of feeding; so that there is in a sense a physiological division of labour within the cell. It is noteworthy that the entoderm nucleus is invariably situated in the inner part of the cell which contains the coarser granules. This position of the entoderm nuclei appears to be not uncommon in embryos where the gastric cavity is filled with food material (compare *Lumbricus*, *t.* KLEINENBERG, and *Planorbis*, *t.* RABL); and RABL has

suggested in the case of *Planorbis* that they play a part in the absorptive activity of the cells. I have not been able to discover any such function in the nuclei.

§ 6. *Comparison with other forms.*

Upon comparing the formation of the digestive cavity in *Renilla* with that of other Anthozoa, we find, in some cases, a close agreement, but in other cases the phenomena are entirely different. All of the Alcyonarian forms, so far as known, excepting *Monoxenia*, agree in their general features with *Renilla*, developing as solid delaminate planulas, in which the gastric cavity is hollowed out by the disintegration and absorption of a central mass of yolk-cells, and the latter are at first indistinguishable from the true or permanent entoderm cells. *Gorgonia*, according to KOWALEVSKY, is an exception to the rule; for the embryo contains a central cavity surrounded by a layer of ciliated rounded cells, which are in turn enclosed in a layer of columnar true entoderm cells. The ciliated cells are believed by KOWALEVSKY to be absorbed, and are considered as homologous with the yolk-cells of other forms. It is noteworthy that *Leptogorgia*, though far more nearly allied to *Gorgonia* than to *Renilla*, agrees entirely in development with the latter, and does not have a permanent segmentation cavity.

Among the Zoantharia, the greater number of forms agree with the Alcyonaria in developing as solid delaminate planulæ in which the gastric cavity is formed by the absorption of a central yolk-mass. A few forms, on the other hand, viz.: *Cerianthus* (KOWALEVSKY, JOURDAN), *Actinia equina L.* (JOURDAN), and perhaps an allied *Actinia*, and probably *Caryophyllium* (KOWALEVSKY), develop as invaginate gastrulæ. BALFOUR states, on the authority of KLEINENBERG, that in some of the apparently delaminate types the segmentation is unequal, which "probably indicates an epibolic gastrula." While the occurrence of epibolic gastrulæ among these forms is by no means improbable, it cannot be accepted on this evidence alone; for the segmentation of *Renilla* shows that such an inference may be entirely false.

It is a curious fact that in two at least of the invaginate forms, viz.: *Actina equina* (JOURDAN), and *Cerianthus* (KOWALEVSKY), a yolk-mass is formed in the gastric cavity some time after the invagination has occurred, though no traces of it exist in earlier stages. Thus, of the former species JOURDAN states: "L'espace entre les cloisons est toujours occupé par une masse probablement vitelline, et qu'on croirait exsudée des tissus de la larve; cette masse nutritive est formée par de grosses vésicules semblables à des cellules adipeuses et par des noyaux fortement colorés par les réactifs."* KOWALEVSKY regards the yolk-mass of *Cerianthus* as a secretion of the deeper layers of the entoderm, and considers its elements as fat globules. In both cases the yolk-mass is eventually resorbed. If the origin of the yolk-mass is correctly described by these eminent observers, it is clearly not homologous with that of the Alcyonarian forms.

* Ann. d. Sci. Nat., 6me série, tome x., p. 129.

The phenomena of the yolk-absorption have not been carefully studied, and it is therefore impossible to draw any general conclusions in regard to the significance of the processes described for *Renilla*. An examination of JOURDAN's descriptions and figures of the larvæ of *Balanophyllia regia* (GOSSE) leaves in my mind little doubt that in this case also the yolk is ingested *Amœba*-fashion by the entoderm cells, though JOURDAN himself puts an entirely different interpretation on his own observations, as may be seen from the following extracts. He says of the entoderm cells at an early stage (*l.c.*, p. 134): "Elles sont très volumineuses, allongées, contiennent des nucléoles fortement colorés par les réactifs *et de grandes vésicules hyalines*. Au centre de la masse vitelline constituant l'endoderme, ces cellules disparaissent, les vésicules hyalines persistent seules" (the italics are my own). In later stages, when six or more septa have appeared: "Sur les coupes transversales, les grandes cellules situées au bord externe de l'entoderme des larves vermiformes ont disparu; les vésicules hyalines persistent et forment la totalité de la masse entodermique." In later stages, however, when the yolk is absorbed, as shown by his figure of the adult entoderm (*l.c.*, fig. 110, plate 15), the cells come into view again, having the same form as before, but rarely containing the "vésicules hyalines."

It appears in the highest degree improbable that the entoderm cells should completely disappear to be subsequently re-developed in precisely the same form. A far more credible conclusion is that the yolk-vesicles are taken bodily into the cells in such numbers as finally to obscure the cell-outlines entirely. The entoderm then seems to have disappeared and only makes its re-appearance when the yolk-vesicles have been assimilated by the protoplasm of the cells. This conclusion is strengthened by the fact that in JOURDAN's figure of the larva of *Actinia equina* (*l.c.*, fig. 119, plate 16) the entoderm cells are figured, before the absorption of the yolk has begun, as clear, well defined, and destitute of yolk-vesicles, while the gastric cavity is completely filled with "vésicules hyalines" precisely like those of *Balanophyllia*. This condition, according to my view, precedes one like the earlier stage of *Balanophyllia* in which absorption has recently begun and in which the entoderm cells resemble those of *Astacus*, as figured by REICHENBACH.*

In all known Alcyonarians the central mass, though at first unsegmented, does sooner or later divide into cells, although many of these perform no active function, become disorganised, and serve only as food for other cells. This indicates that the yolk-cells are the descendants of cells which were once of structural significance; for otherwise their formation and subsequent disintegration would seem to be a sheer waste of energy. They are identical in origin and structure with the permanent entoderm cells, and are undoubtedly homologous with the latter. Hence we may infer that the yolk-cells were originally functional entoderm cells in which deutoplasm accumulated to such an extent that they became devoted solely to the storing of food for the embryo. The remaining entoderm cells retained their functional

* Zeitschr. für Wiss. Zool., Bd. xxix., 1877.

activity as digestive cells, and by an early development of this function in the embryo became capable of digesting the yolk-cells precisely as if the latter were foreign food-matters introduced through the mouth. How such a two-fold specialisation of the entoderm cells was possible is shown in the embryo of *Gorgonia*; for in this case the yolk-cells still persist in an apparently functional state, being ciliated and surrounding a central cavity. Only a step before this is the planula of *Gorgonia* or *Liriope* (Metschnikoff and Fol) in which the central cavity exists from the first and all the delaminated entoderm cells persist as such.

If we push this speculation further and inquire after the causes which originally determined that some of the primitive entoderm cells should persist as such while others became yolk-cells, we encounter a very broad question, which it would be hardly profitable to enter upon here, since it belongs too exclusively at present to the region of pure speculation. The question is of the same nature, for instance, as that concerning the influence which determines the survival of a particular cell of the germinal epithelium of the ovary, as an ovum, while its neighbours are absorbed, or remain as simple epithelial cells.* We can only say that the differentiation probably stood in some relation with the relative position of the cells; for only the peripheral cells persist as entoderm cells. This suggests that the divergence may have depended upon, or is at least now directly determined by, differences in the supply of oxygen afforded to the cells—in other words is due to respiratory differences. The peripheral cells being nearer to the exterior, must command a more plentiful supply of oxygen, and in this respect have a decided advantage over the inner cells. This may be enough to determine the survival of the former and the disintegration of the latter.

According to a theory of Weissmann's, the cells of the ovary (in *Leptodora*) attain a certain "maximal development," which is a critical point in the life of a cell. If it receive an additional impulse, though a very slight one, it continues to develop into an ovum at the expense of its less fortunate neighbours. If, on the other hand, it does not receive this impulse, the cell loses its power of development and is absorbed by the developing ova. The determining impulse is believed by Weissmann to be a slight advantage of nutrition which is potent because acting at a critical moment. Such a theory of "maximal development" would seem to apply well in the present case, but the impulse to development does not seem to be in any way connected with general nutrition but only with the supply of oxygen. The theory, though resting perhaps on a rather slender basis, has the merit of showing how a very slight difference in the supply of oxygen might determine the survival or the degeneration of the cells.

* See on this point Weissmann, "Ueber die Bildung von Wintereiern bei *Leptodora hyalina*," Zeitz. f. Wiss. Zool., Bd. xxvii., 1876, who has given an elaborate discussion of the question in the case of the ova of the Cladocera.

§ 7. *Changes in the ectoderm and formation of the supporting lamella.*

In the larva of eight hours, as already described, there is a delicate sinuous membrane lying between the ectoderm and entoderm, upon which the cells of the former are planted as upon a basement membrane. This is perhaps the first beginning of the characteristic supporting lamella, but it is far less well defined and less conspicuous than in later stages, and the great bulk of the lamella is formed somewhat later by a peculiar transformation of the inner ends of the ectoderm cells. It is difficult to determine the origin of this preliminary membrane, but appearances indicate that it is secreted by the expanded bases of the ectoderm cells. The membrane varies much in appearance and is sometimes quite invisible even in much later stages. It is often apparent in one part of a section and quite invisible in other parts, while the true lamella, once formed, is remarkably constant and distinct.

The ectoderm cells of this stage have a high columnar form, which, though ultimately lost, is retained throughout the succeeding stages until a late period. At intervals, however, the cells rapidly proliferate (fig. 131, twenty-eight hours), and the columnar form may at these times be temporarily lost, the cells assuming various rounded forms and becoming in many cases entirely separated from the underlying entoderm cells. The division of the cells takes place both in horizontal and vertical planes, so that the ectoderm gradually becomes several layers deep. At the close of a period of proliferation most of the cells resume the high columnar form, some of them extending through the entire thickness of the ectoderm, others extending inwards from the surface and terminating by attenuated extremities without reaching the entoderm. Others, again, are placed with their broader end—which contains the nucleus—lying near the bottom of the ectoderm, and others still are of a fusiform shape with the thickest part containing the nucleus, near the middle of the ectoderm. The structure of the ectoderm at this stage is very like that of *Heliopora* (Moseley, Phil. Trans., Vol. 166, 1876).

Besides the columnar cells there are others of a rounded form with centrally placed nuclei, which lie in the deeper parts of the ectoderm or in the narrow clear space which often separates the layers; they often lie directly on the outer ends of the entoderm cells. These never return to the columnar form and persist throughout the entire development. They give rise to elements of the so-called mesoderm, some of them becoming the matrices for the development of the spicules, and others remaining as peculiar rounded cells which are possibly nerve-cells.

In the larva of about twenty-two hours (figs. 125, 132), the basal ends of the columnar ectoderm cells undergo a peculiar change of form and structure. They separate completely from the entoderm, become smoothly rounded, the character of the granulation changes, and they stain less readily than before. At the same time a large quantity of a finely granular substance makes its appearance in the space between the ectoderm and entoderm (figs. 125, 133). This space is sometimes very

wide on account of the shrinkage of the central mass, but even in this case is sometimes nearly filled with the granular matter. The appearance of the granular mass varies greatly in different specimens and in different parts of the same section. It may be very abundant and of a loose flocculent character in one part, while elsewhere it gradually disappears and is replaced by a definite membrane lying between the ectoderm and entoderm, which is unmistakably the supporting lamella. In favourable specimens the granular mass may be traced around the section, becoming more and more closely compacted until it passes directly into the supporting lamella.

These facts leave no doubt that the supporting lamella is derived from the granular mass, which becomes compacted together to form a definite membrane. The granular mass probably never has naturally any considerable thickness, being compacted into the membrane as soon as it is formed. The loose flocculent character is probably produced by the action of the reagents which causes the material of the supporting lamella to swell up, while the central mass at the same time shrinks away from the ectoderm, forming the cavity in which the granular mass lies.

In fig. 133, which will illustrate the appearance of a section at this period, there are parts of the section where neither granules nor lamella appear, other parts where the outer ends of the entoderm cells are covered only by their own cell-membranes outside of which is a small quantity of granular matter; while in other portions a pretty distinct lamella is formed with abundant granular matter outside of it. The entoderm cells show no change at any time during the formation of the lamella. This indicates that the ectoderm alone is concerned in the production of the granular matter which forms the lamella, and this conclusion is confirmed by a study of the ectoderm cells. The inner ends of the cells are rounded and swollen and often terminate in knob-like swellings (fig. 132, *b*.), attached to the bodies of the cells by narrow necks. These swollen inner ends then separate from the bodies of the cells and lie in the deeper parts of the ectoderm or in the space between the two layers. In some specimens, of which fig. 132 is a good example, the lower part of the ectoderm is closely packed with these rounded bodies, of which some are still attached to the cells, but most are free. The substance of which these balls are composed is quite like the granular substance, and the balls may be seen in various stages of disintegration.

Hence we may conclude that the material of the supporting lamella is derived from the disintegrated granular balls which have separated from the ectoderm cells. It is possible that the swollen inner ends do not normally separate bodily from the ectoderm cells and that this is accidentally done in making the sections. This is hardly probable, however, since the outlines of the granular masses are usually regular, and they are found free in large numbers. The granular bodies appear in some cases to discharge their contents without breaking down and losing their form. I conclude this from the occasional presence of clear, rounded bodies in the granular mass of the same form and size as the granular bodies. These clear bodies (several of which are shown in fig. 133)

appear to be surrounded by delicate membranes and become in some cases incorporated into the substance of the supporting lamella. They are not to be confounded with the rounded nucleated cells which are sometimes also found in the granular mass and may likewise become incorporated into the lamella. Besides the latter, cellular elements derived from the entoderm may in some cases enter into the composition of the lamella. Now and then an entoderm cell (see figs. 125 and 132) may flatten down, become incapable of development and become incorporated with the mass of the lamella.

After the secretion of the granular matter is completed the cells re-assume their high columnar form with their inner ends often resting upon the lamella as on a basement membrane (figs. 127–130). The latter appears as a very distinct, narrow, structureless membrane sharply separated from the ectoderm and entoderm. Outside of it is usually a narrow, clear space, but the granular matter has entirely disappeared. This condition of the ectoderm is maintained until the sixtieth or seventieth hour, when the ectoderm totally changes its character. The lamella remains unchanged up to the latest stage of the colony observed, without increasing in thickness or undergoing visible change of structure.

Review.

The material of the lamella is derived from the cells of the ectoderm by a peculiar form of cuticular secretion, which consists in the separation of rounded granular masses from the inner ends of the cells. The formation of these bodies is a process entirely different from cell-division since the nuclei do not divide, and they remain quite unchanged during the process. The granular bodies in most cases disintegrate, but sometimes appear to discharge their contents as in ordinary secretion. Possibly the ectoderm cells may also in some cases discharge the contents of their swollen basal ends without the separation of a part of the cell, but this must, I believe, be exceptional. The mode of secretion described is a very anomalous one, and appears to stand midway between the disintegration and discharge of an entire cell during secretion, as in the formation of "goblet-cells" in mucous glands, and the more usual forms of secretion in which the product exudes from the cell without the destruction of the latter.

The formation of the supporting lamella in other forms has not been worked out with sufficient care to afford any basis for comparison. KOWALEVSKY concluded that the lamella in *Actinia* is secreted by the entoderm, since it penetrates into the septa, which are entirely entodermic. This is, however, an unwarrantable conclusion; for, as will be shown later, the lamella of the radial septa has an entirely different origin from that of the peduncular septum, and both differ in origin from that of the body-wall. It is evident that the supporting lamella, though probably containing cellular elements derived both from the ectoderm and entoderm, is not in any sense a special mesodermic layer, but has only the significance of a structureless cuticular membrane separating and supporting the two fundamental layers of the body.

II.

DEVELOPMENT OF ORGANS AND TISSUES.

The larva now consists of a layer of ectoderm and entoderm separated by the supporting lamella and enclosing the gastric cavity. The latter has as yet no communication with the exterior and shows no trace of division into the eight radiating chambers characteristic of all Alcyonarian polyps. Within a few hours—usually between the fortieth and fiftieth—the œsophagus is formed, though it is not perforated until a far later period, and the gastric cavity is divided into chambers through the appearance of radiating septa. These structures develop simultaneously, but it will be convenient to follow their formation separately, and the same plan will be followed in describing the development of other organs.

§ 8. *Formation of the œsophagus and mouth.*

The œsophagus usually makes its appearance in the larva of about forty hours as a solid invagination of ectoderm at the larger end of the body (fig. 134). The high columnar ectoderm cells at this point change their form entirely and rapidly multiply, and are pushed into the body of the larva as a solid plug (fig. 134, *st.*). The invaginated cells are very small, rounded, possess distinct but very small nuclei, and are so closely packed together that their outlines can scarcely be distinguished except in very thin sections. They differ widely from the entoderm cells, being far smaller, staining more deeply and of a different tint, and their nuclei are much smaller. In some cases the œsophagus contains from the first a very small cavity extending inwards from the exterior, but it is usually quite solid. As the plug of ectoderm is pushed in, it carries before it the supporting lamella and the entoderm, the cells of the latter multiplying at the same time. These entodermic cells assume a high columnar form, with their long axes directed towards the œsophagus (fig. 134).

The ectodermic plug grows rapidly backwards and assumes a somewhat pyriform shape from the expansion of its lower extremity (fig. 136), and the entoderm, which everywhere covers it, often becomes much thickened, especially at its lower end. A narrow cavity (fig. 135) then appears in its centre, communicating at the anterior extremity with the exterior, but still ending blindly below. The cavity appears to be formed by the giving way of the central cells, aided to some extent, perhaps, by absorption. In this stage the cells towards the outer opening sometimes have an obscurely columnar form, but towards the inner end of the invagination are small and rounded as before. The cavity at its very first appearance, as shown in transverse sections, is greatly elongated in a particular direction, which is always the same in relation to the septa and is shown by the later development to coincide with the dorso-ventral axis.

The œsophagus remains in this condition for a considerable period (twenty to twenty-five hours), during which the only change consists in the clear definition of the cavity and the expansion of its lower end (fig 136). In most cases the lower angles of the cavity are prolonged downwards so that the cavity has a distinct Y-shape; this form is sometimes much more pronounced than in the figure. The cavity then breaks through, thus placing the gastric cavity for the first time in communication with the exterior.

I have made many sections, longitudinal and transverse, through the œsophagus at this period, a study of which leaves little doubt that great variation exists in the formation of the mouth, as in so many other features of the development. The most common mode is illustrated by figs. 137–140. The wall of the œsophagus thins away by absorption at one of the lower angles of the Y (fig. 131) and finally breaks away at this point (fig. 139). At the opposite side the mass of tissue forming the bottom of the œsophagus still remains attached to the lateral wall of the œsophagus and to the edges of the septa which have meanwhile been formed. As the septa grow backwards this mass of tissue (which for the sake of convenience I shall call the *œsophageal plug*) is carried down with them, being attached to the edges of one or more of them (fig. 140), sometimes by a narrow neck. The mass of tissue is then gradually absorbed and the œsophagus is left in free communication with the gastric cavity. In several of my specimens, at this stage, a large mass of tissue may be observed lying in the gastric cavity below the œsophagus. This is quite similar in appearance to the œsophageal plug, and is, I believe, identical with it. Hence it would appear that in some cases absorption takes place all around the œsophageal plug, which finally drops out bodily into the gastric cavity and is there absorbed as if it were food or yolk-material. In a number of specimens, one of which is shown in fig. 141, a still different mode was observed. Absorption here begins near the middle of the bottom of the œsophagus between the two arms of the Y-shaped cavity and the opening at length breaks through at this point, leaving the remains of the œsophageal plug attached to the lips of the œsophagus where they are absorbed.

During these changes the layer of ectoderm forming the bottom of the œsophageal cavity becomes indistinct, and in most cases the supporting lamella which separates it from the underlying mass of entoderm disappears. The cells of both layers in the plug change their character and are no longer differentiated by the staining fluid, so that the œsophageal plug appears to be composed of uniform confused granular cells. In one of my specimens (fig. 159) the greater part of the œsophageal plug seems to have been absorbed, leaving the supporting lamella stretching across the œsophageal cavity. Below this is a mass of delicate *débris*, which is apparently the last remains of the œsophageal plug.

Review.

The earlier view, according to which the œsophagus is to be regarded as a stomach, opening below into the body cavity, is now entirely abandoned. In view of its

embryological history, the œsophagus is apparently a true stomodæum, comparable to that of the higher Metazoa. The general occurrence of this structure—which, so far as the evidence at command shows, is homologous throughout all the groups in which it is found—is a very striking fact which probably has an important phylogenetic significance. Its universal occurrence among the Anthozoa and complete absence from the Hydrozoa is a strong argument in favour of the more primitive nature of the latter group. From the fact that the Anthozoa are the most primitive group in which the stomodæum appears, it might be concluded that this group represents the stock from which the higher Metazoa have descended. It seems, however, much more probable that the line of descent has been through some primitive Turbellarian form which, in common with the polyps, derived the stomodæum from a still earlier group. What this origin of the stomodæum was is still an unsolved problem. The hypothesis that the stomodæum is to be regarded as the introverted manubrium of a Hydrozoan, though a plausible one, has no embryological facts in its favour, and can hardly be accepted without additional evidence.

§ 9. *Development of the septa.*

The septa make their appearance at about the same time with the stomodæum, and are well developed within a few hours. As we shall see below, the eight radial septa of the anterior part of the body, which are characteristic of all Alcyonaria, differ entirely in structure and mode of origin from the peduncular septum, a structure which is found in the Pennatulacea alone. Hence it will be convenient to describe separately the development of the two forms of septa.

a. Formation of the radial septa.

Although the peduncular septum makes its appearance some time before the radial septa, it is preferable to describe the development of the latter first. They make their appearance simultaneously at the oral extremity of the larva at the time when the stomodæal invagination takes place, and gradually extend thence backwards about to the middle of the body. Although I have made many sections through the septa at the time of their first appearance, and have given special attention to the matter, I have not been able to discover any difference in the time of their appearance. In later stages, as described further on, they are of different lengths, and the differences are perfectly constant. This is, however, the only indication of a regular succession in the development of the septa, and in the earlier stages no difference can be observed.

The septa appear upon longitudinal section (fig. 136, fifty-two hours) as thick plates of entoderm cells (*s.s.*) extending downwards from the oral end and ending by free edges below. Inwardly they are continuons with the entoderm covering the stomodæum; outwardly they join the entoderm of the body-wall. In transverse section (fig. 142) they are seen to radiate at nearly equal intervals from the stomodæum. The centre

of each is occupied by a delicate supporting lamella, continuous outwardly with that of the body-wall, and inwardly with that which separates the ectodermic and entodermic layers of the œsophagus. The entoderm cells are arranged upon both sides of the lamella in a thick irregular layer. They are of an elongated pyriform shape, and are so large and closely packed as to fill up entirely, in most cases, the spaces between the septa. In one or two of the compartments, however, a small space appears near the middle, the cells radiating towards it in all directions from the septa, body-wall, and œsophagus. These spaces constantly increase in size as development proceeds, and form the radiating chambers which surround the stomach. The cells are so closely packed at first that a longitudinal section in nearly any plane gives the appearance of fig. 136, the entoderm having the appearance simply of being greatly thickened in the oral region.

Anteriorly the septa extend quite across the gastric cavity from the œsophagus to the body-wall, as shown in the figure. Behind the œsophagus their inner edges are free and the septa appear in transverse section as low ridges which scarcely rise above the level of the general layer of entoderm. They may, however, be readily recognised by the presence of the central layer of supporting lamella and the radiating disposition of the cells over them. This is shown in fig. 143, which represents a section from the same larva (forty-eight hours) with fig. 142 taken farther back at the lower end of the œsophagus. Three of the septa still reach the œsophagus (*a*.), two are barely united with it, and two are separated from it by considerable intervals. As development proceeds the septa become constantly thinner and the intervening chambers increase correspondingly in size. This is effected partly through the increasing size of the larva and in part by a change of form in the entoderm cells covering the septa, which become far less elongated. Fig. 144 represents a section through the anterior part of a four days' larva in which the radiating chambers have attained a considerable size. Fig. 145 is from the same specimen at the posterior end of the œsophagus; this corresponds very closely with the earlier stage shown in fig. 143. Fig. 146 is from the same specimen still further back, showing the free septa. The bilateral arrangement of the septa is strikingly shown in the symmetrical disposition of the septa of different widths (see p. 764). The entoderm cells have entirely changed their form, being now more or less flattened, or even forming in some places a flat pavement epithelium. On the edges of the septa have appeared the mesenterial filaments (*f.f.*) but a description of these may conveniently be deferred to the following section.

I have studied carefully the young septa for evidence of the participation of the ectoderm in their formation, but am led to conclude that they are formed almost exclusively from the entoderm, though in some cases a few ectoderm cells may make their way into the outer parts of the septa. In the youngest septa observed, the supporting lamella almost always appears as a simple membrane joining the lamella of the body-wall nearly at a right angle, and sometimes without interrupting its outline (fig. 147). In most cases, however, the lamella of the body-wall bends inwards

slightly at the point where the septum meets it, and ectoderm cells with conspicuous nuclei may sometimes be seen lying directly in the angle thus formed (fig. 148.) (This figure is from the peduncular septum, but answers equally well for the radial septa.) In a very few cases the lamella appears to be actually infolded to some extent at the base of the septum, and ectoderm cells pass into the space thus formed, and thus come to lie within the body of the septum. In still other cases this fold appears to close up, forming a small triangular space at the root of the septum in which one or two ectoderm cells appear, as shown in fig. 149, *n*. These never extend far out into the septum, however, and the greater portion of the lamella of the latter is secreted, as I believe, by the bases of the entoderm cells.

The question as to whether the lamella of the septum is double, and contains ectoderm cells invaginated from the exterior, is one of much theoretical interest, since, if this be the case, the septa are to be regarded as actual infoldings of the entire body-wall, and not as simple entodermic ridges. LACAZE-DUTHIERS in his beautiful memoirs on the development of polyps,* expressly states that both of the layers of the body-wall participate in the formation of the septa, and he figures in the larvæ of *Astroides calycularis* ectoderm cells with numerous nematocysts passing directly into the body of the septum. On the other hand, he is strenuously opposed by KOWALEVSKY, who maintains that the entoderm alone is concerned in the formation of the septum. My own observations throw no new light on this interesting question; for although the great bulk of the septum with its lamella is in *Renilla* certainly entodermic, yet the occasional entrance of a few ectoderm cells into the base of the septum may indicate that an invagination of ectoderm originally occurred, in connexion with a special development of the underlying entoderm, but was subsequently nearly or completely lost. The matter is certainly worth further investigation in other polyps, for it is difficult to believe that LACAZE-DUTHIERS's figures rest upon no other basis than pure imagination.

b. Arrangement of the septa.

The septa are grouped about the œsophagus with a definite relation to the dorso-ventral axis, as shown in transverse sections (fig. 142). The cavity of the œsophagus is elongated in the dorso-ventral axis, and its angles are opposite two compartments, which may in KÖLLIKER'S terminology be called the dorsal and ventral chambers. On each side of the œsophagus are, therefore, three chambers which are called respectively the dorso-lateral, median lateral or simply lateral, and ventro-lateral chambers. Following the same terminology, the septa may be designated as dorsal, dorso-lateral, ventro-lateral and ventral, respectively, there being four on each side of the œsophagus.

This bilateral grouping of the septa becomes very conspicuous in transverse sections

* Arch. de Zool. Exp. et Géner, tome i., ii.

below the œsophagus in later stages. In the four days' larva (fig. 146) the septa are clearly seen to be arranged in pairs on opposite sides of the dorso-ventral axis. The dorsal septa (*d.s.*) are very narrow and widely separated, and have no mesenterial filaments on their edges, the dorso-lateral (*d.l.s.*) are much wider, and are thickened at their edges to form the mesenterial filaments; the ventro-lateral septa (*v.l.s.*) are widest of all, and the ventral septa (*v.s.*) are about equal to the dorso-lateral.

When the septa are sufficiently far advanced to be visible from the exterior upon rendering the larva transparent by reagents or by compression in the fresh state, they are found to have a remarkable and definite arrangement. This arrangement is apparent at a very early stage, and remains unchanged as far as the development can be followed. Hence it will be convenient to describe it from a somewhat older specimen (figs. 103, 104, four days). The dorsal septa (*d.s.*) extend backwards for about one-fourth the length of the body, where they are joined by the dorso-lateral septa (*d.l.s.*). From their point of union the peduncular septum (*p.s.*) extends backwards to the aboral end of the body. The ventro-lateral septa (*v.l.s.*) extend backwards some distance beyond the point of union of the above-mentioned septa, and then bend upwards to join the peduncular septum at the point *u* (fig. 104). In some cases it is difficult to trace the septum up to the peduncular septum, especially when the larva is fully expanded. In fact, I completely overlooked their connexion in my earlier paper, and described the septum as terminating freely below. In some specimens this appears to be actually the case, though it is difficult to make sure of it, but in every case the line of longitudinal muscles accompanying the septum (see p. 780) is continued up to the peduncular septum. The ventral septa (*v.s.*) are of nearly the same length as the dorsal, and in some specimens appear to terminate freely below. In most cases, however, careful examination during a half-contracted state of the larva shows that the lower ends of the septa bend towards one another and unite in the median ventral line. From their point of union a band of longitudinal muscles extends backwards in the median line of the body. In specimens where the septa themselves do not actually join, the lines of accompanying muscles bend towards one another and unite in the same way that those of the ventro-lateral septa join the peduncular septum.

The arrangement of the septa shows, therefore, a very marked bilateral symmetry, the septa being disposed according to their width, length, and relations to each other, in pairs which are symmetrically placed with reference to the dorso-ventral plane.

c. Formation of the peduncular septum.

The peduncular septum has a quite different mode of origin from the radial septa, though it is continuous with the latter at their earliest appearance. It makes its appearance at about the fortieth hour at the *posterior* end of the body, sometimes, at any rate, before the stomodæum or the radial septa are formed. A longitudinal section through this part of the body of a forty-hour larva is shown in fig. 150. The

rudiment of the peduncular septum (*p.s.*) appears as a rounded mass of entoderm cells, at the base of which is a delicate supporting lamella running inwards from the lamella of the body-wall, and becoming insensibly lost among the cells. The anterior part of the stomach still contains a considerable quantity of unabsorbed yolk, and the stomodæum is just beginning to be formed. From this point the septum grows rapidly forwards, ending by a free edge in front. As the septum extends forwards its lateral portions grow more rapidly than the middle, so that the free edge becomes deeply concave in front. I have no figures of this in early stages where it is most pronounced; it is shown in fig. 136 at *e*, where it has extended very far forwards.

By reason of this structure of the septum, the posterior part of the body is completely divided into a dorsal and ventral chamber (fig. 154); while farther forwards, in front of the edge of the septum, the gastric cavity is undivided, and a section shows only the lateral forward extensions of the septum (fig. 154, *a.*, *a.*). These have exactly the appearance of two independent septa, situated on opposite sides of the body. If they be traced forwards they are found to be continuous with the dorsal septa at their point of union with the dorso-lateral pair, as explained at p. 765. The free edge gradually extends forwards until it reaches the point at which the lateral portions join the radial septa, and then remains stationary for a long period. Its subsequent development is described at p. 795.

A transverse section through the peduncular septum behind its free edge (fig. 151) shows that it is composed mainly of two thick layers of clear, rather ill-defined entoderm cells, separated by a peculiar membrane (*ax.*). At the sides this membrane appears like the ordinary lamella of the septa, and joins the lamella of the body-wall. Towards the middle, however, the membrane splits into two layers enclosing a narrow space in which appear numbers of conspicuous nuclei similar to those of the entoderm cells. Cell-outlines can only faintly be distinguished, but there can be no doubt that the nuclei belong to cells which are enclosed in the lamella and may conveniently be termed the *axial cells*. These cells are confined to the central portion of the septum behind the free edge. The forward extension of the lateral parts of the septum show no trace of anything like the axial cells in their lamella. As development proceeds, the axial cells become more and more flattened between the enclosing layers of lamella and at length nearly or quite disappear (fig. 173, *p.s.*). The lamella of the peduncular septum has then the same appearance as that of the radial septa in which no axial cells were ever observed.

In order to ascertain the origin of the axial cells it is necessary to study sections of still earlier stages of development. Fig. 153 represents a longitudinal section of a somewhat younger larva (forty-eight hours). The entoderm cells forming the main mass of the septum are here very distinct and of a high columnar form. The axial cells are larger and their outlines are more distinct. Their appearance is more clearly shown in fig. 136, from another specimen. The lamella is simple behind but splits further forwards into two delicate membranes between which lie the axial cells. The latter

are clear, with very delicate, rounded or polygonal outlines, and with very conspicuous intensely stained nuclei, which are quite similar to those of the entoderm cells (*en.*). Towards the free edge of the septum (*e.*) the two layers of the lamella disappear and the axial cells become confounded with the entoderm cells.

The latter point is most clearly shown in transverse sections taken just behind the free edge of the septum (fig. 152). We find here that the lamella of the lateral portion is simple as in the radial septa, but further inwards the lamella splits into two layers between which lie a number of closely packed axial cells. Still farther inwards the layers of the lamella entirely disappear and the axial cells graduate insensibly into the rounded entoderm cells which form the edge of the septum. In the section immediately behind this, the layer of axial cells can be traced quite across from one side to the other, but they lie several cells thick in the middle and are scarcely distinguishable from the adjoining entoderm cells. In sections further forwards the septum entirely disappears and the body of the larva consists of an unbroken layer of ectoderm and entoderm enclosing a nearly solid mass of yolk.

These sections show very clearly that as the septum grows forwards the entoderm cells of which it is composed arrange themselves in three layers. The two outer layers persist as the entodermic covering of the peduncular septum, and form its main bulk; the cells of the middle layer atrophy, flatten together, and form the axial cells. The two layers of lamella which enclose the axial cells are no doubt secreted by the adjoining entoderm cells; the appearances indicate that these membranes are simply the confluent and much thickened membranes of the cells.

As in the case of the radial septa, I have studied with care the possibility of ectodermic cells passing into the septum at its lateral parts where it joins the body-wall, but have been unable to find decisive evidence of such a process. The sections show exactly the same appearances as those of the radial septa. The lamella of the septum sometimes joins that of the body-wall abruptly, without any infolding of the latter; in other cases the lamella of the body-wall is somewhat infolded, and the angle thus formed contains ectoderm cells; in other cases, again, a small triangular space appears at the root of the septum, enclosing one or two cells. The latter are quite similar to the ectoderm cells which appear in the last-described case, and seem to have been introduced from the outside. In rare cases, one of which is carefully represented in fig. 156, the lamella has the appearance of folding in so as to leave a narrow connexion between the cleft containing the axial cells and the ectodermic layer. From these appearances I conclude that the ectoderm cells may in some cases actually pass into the septum by an infolding of the lamella, but they can never do so in considerable numbers, and take only the most insignificant part in the formation of the septum. Far the greater part of the peduncular septum, as of the radial septa, is formed from entoderm cells alone. Misled by certain theoretical considerations, I was at first strongly inclined to regard the axial cells as ectodermic in origin, having been invaginated from the exterior in a fold of the lamella. More careful study

entirely disproved this view. The entodermic origin of the axial cells is placed beyond all doubt, by the fact that typical entodermic spicules are sometimes developed in them. These are unmistakable in form and optical characters, and are never developed in ectoderm cells.

In its earlier stages the peduncular septum forms a complete partition, extending from side to side, and reaching the posterior end of the body. At a later period it becomes perforated along its sides, and at its posterior extremity by rounded openings, which place the chambers of the peduncle in communication. The posterior opening (fig. 155, *p.*) becomes very large, and the lateral openings (*o.*) also increase in size, until the septum has the appearance of being suspended by narrow threads from the lateral walls of the peduncle (see figs. 181, 182). The lateral openings subsequently become much reduced in size, or even close entirely (figs. 206, 207), but the posterior opening remains permanently in the adult, and has been described and figured by KÖLLIKER.

In *Leptogorgia* the eight radial septa are visible when the larva ceases to swim, and attaches itself to the bottom (fig. 113). So far as could be determined, they develop simultaneously, and extend throughout the entire length of the body, without joining one another, or otherwise departing from a strictly radial disposition. They have, however, the same bilateral arrangement with respect to the œsophagus as in *Renilla*. The mouth and œsophagial cavity are distinctly elongated in a definite plane, which may by analogy be regarded as the dorso-ventral. Nothing like the peduncular septum in its fully formed condition was observed, but there is an accumulation of entoderm cells at the aboral end of the larva (fig. 116), developed in connexion with the axis, which is very similar to the peduncular septum in its earliest stages.

Review.

The radial septa and the peduncular septum are structures widely different from one another in structure and origin. The former have a simple cuticular supporting lamella, consist of two strata of entoderm cells, arise at the anterior extremity of the body and grow backwards; the latter, on the other hand, has a double supporting lamella, consists of three layers of entoderm cells, arises at the posterior end of the body and grows forwards.

The eight radial septa are of universal occurrence among the *Alcyonaria*, have in all cases the same grouping about the œsophagus, possess an entirely similar musculature, and for these reasons are clearly homologous throughout the group. I had strong hopes that a careful study of the early development of the radial septa might give some indication of the relation in which they stand to the septa of other groups of polyps. The result is, however, a purely negative one, and affords absolutely no new basis for speculation upon the systematic affinities of the *Alcyonaria*. Their

development is greatly condensed and abbreviated, and shows not the slightest indication of any such remarkable and regular sequence as that which LACAZE-DUTHIERS has shown to characterise the development of the septa in various representatives of the Zoantharia.* In this respect *Renilla* agrees with all the Alcyonaria whose embryonic development has been investigated, though observations on this matter are so scanty as to afford no satisfactory basis for comparison. In the case of *Alcyonium*, KOWALEVSKY was unable to make out the succession of the septa, but he states that it seemed to be analogous to that of the Zoantharia, as described by LACAZE-DUTHIERS. This statement is, however, too vague to be of any value.

The lateral forward extensions of the peduncular septum (fig. 154) have precisely the same structure as the ordinary septa, and they are continuous anteriorly with the dorsal pair of septa. Hence there can be little doubt that the peduncular septum is to be regarded as formed by the union of the dorsal pair of radial septa, beginning at the posterior end and extending thence forwards. It is highly probable that all of the septa in *Renilla* originally extended to the posterior extremity of the body; for this is the case in the larval *Leptogorgia* and in nearly all other polyps (*Cerianthus* excepted). The six ventral septa have ceased to extend as far as the posterior extremity, but the primitive condition has been retained by the dorsal septa and they have furthermore united by their inner edges to form a flat plate, the peduncular septum.

The axial cells, according to this view, are to be regarded as having been formed along the line of union between the two septa by a peculiar arrangement of the entoderm cells in this region (see fig. 152). Before considering the cause of such an arrangement, it is necessary to look for the homologue of the peduncular septum in other Pennatulids. As has already been stated, no homologous structure is known to exist, except in the Pennatulacea; but its homologies in this group appear tolerably clear although they cannot be determined with certainty without further embryological investigation. KÖLLIKER has described with great care the structure of the peduncle in many species of Pennatulids. The most usual and typical structure is as follows. The cavity of the peduncle is divided by four septa into four chambers of which two occupy a lateral position, the third is dorsal, and the fourth ventral. The four septa meet in the middle of the peduncular cavity, forming a central mass within which lies the axis enclosed in an epithelial sheath. Toward the posterior end the two lower septa become free from the body walls and run out upon the hinder end of the axis which lies free in the peduncular cavity. A part of each upper septum likewise extends out upon the free extremity of the axis, but the remaining parts of the upper septa fuse together to form a single transverse septum which runs backwards to the tip of the peduncle and thus divides the latter at its posterior end into a dorsal and a ventral chamber. (For a full description of this very peculiar arrangement, which can scarcely be described without figures, see KÖLLIKER's 'Pennatuliden,' p. 23).

* Arch. d. Zool. Exp., tome i., ii.

What the relation of these four septa is to the axial polyp is quite unknown, owing to the complete lack of anatomical studies of very young Pennatulids. Through what process the lower end of the axis comes to lie free in the peduncular cavity is also unknown. But it seems highly probable, as KÖLLIKER remarks (*l.c.*, p. 270) that the peduncular septum of *Renilla* is homologous with the single horizontal septum (*septum transversale* of KÖLLIKER) of the posterior part of the peduncle in other Pennatulids. This homology appears especially clear in the case of *Renilla amethystina* (VERRILL); for in this case, the extreme anterior part of the peduncle is divided as in the Pennatulidæ into four chambers, which clearly correspond to the four longitudinal canals of the latter. A section through this part of the peduncle (which is situated near its anterior end and forms in reality a part of the disc) is very similar except in the lack of an axis to a section through the four chambers of *Pennatula* (see fig. 72, plate 8, KÖLLIKER). The two additional chambers of *Renilla amethystina* are laterally placed, and are developed apparently as a pair of cavities in the substance of the peduncular septum. The four partitions which thus arise are all continuous behind with the single horizontal septum.

This comparison appears to me to be well founded, though it cannot be proved so without the aid of further embryological studies. If it is so, *Renilla amethystina* is a perfect connecting link, so far as the structure of the peduncle goes, between *R. reniformis* and the axis-bearing Pennatulids.

In all the latter forms the axis, when present, is suspended by these four septa, and it is difficult to understand their appearance in *Renilla amethystina*, except on the supposition that in this form an axis once existed, but was subsequently lost. In *R. reniformis*, the four septa also have disappeared, leaving only the peduncular septum as the representative of the *septum transversale*. This view is supported by the development of the colony which, as pointed out in section 19, indicates the derivation of *Renilla* from an axis-bearing form, resembling the *Bathyptileæ*.

As a matter of fact, we find the axis developed in very different degrees in the various genera of the Pennatulids; and in certain of the *Veretillidæ*, as *Clavella* or *Cavernularia*, the axis is very small or, even in some species of the same genera, quite absent. Whether the rudimentary condition or total want of an axis in these forms is due to the gradual loss of an axis cannot be determined; but the probabilities certainly appear to be in favour of such a view, since these genera have a much less primitive structure in some other respects than some of the axis-bearing forms. We are perhaps able to get some idea of how the axis might be gradually lost. Since the axis ends at some distance from the tip of the peduncle, a certain amount of movement is still permitted to the latter; and the great development of the peduncular muscles indicates that this power of movement must be an important factor in the life of the organism. In *Renilla* the power of movement is of vital importance (see p. 784), and an axis would be of no conceivable use. It is easily conceivable that the power of movement might become of paramount importance to one of the axis-bearing forms,

and the presence of a rigid axis would in such a case be disadvantageous. Hence we can see how, by natural selection, the posterior muscular part of the peduncle might be constantly increased in size and importance, accompanied by a corresponding reduction of the axis. If this process were continued until the axis disappeared, a condition would result like that shown in *Renilla amethystina*, and by a further reduction the structure of *R. reniformis* would be attained, in which the dorsal and ventral chambers and the *septum transversale* alone remained.

The foregoing considerations strongly suggest that the peculiarities in the structure and formation of the peduncular septum may be in some way a result of the former existence of an axis. It is, however, useless to speculate on this matter so long as the development of the axis in the typical Pennatulids is unknown; and in regard to this, in KÖLLIKER'S words, "mangeln alle und jede Erfahrungen."

Two entirely different views of the Pennatulid axis have been entertained. KÖLLIKER, on the one hand, regards it as of mesodermic origin, the mesodermic elements being supposed to be originally derived from the entoderm. To quote his own words ('Pennatuliden,' p. 428): "Anders bei der Kalkaxe, denn hier spielt ein osteoblastenähnliche Zellenlage, deren Abstammung von dem Entoderma zwar wohl sicher vermuthet werden darf, aber noch nicht nachgewiesen ist, eine Hauptrolle." On the other hand, KOCH considers the axis as probably ectodermic in its origin. This author, while admitting the so-called axis of a certain division of the Gorgonacea (Pseudaxonia) to be mesodermic, has given very strong reasons for the belief that the true axis of many Alcyonaria is secreted by a layer of epithelial cells directly derived from the ectoderm. KÖLLIKER himself observed that in some of the Pennatulida (*Pteroides*, *Virgularia*) the axis is surrounded by a distinct epithelial layer, and KOCH has shown that this is the case not only in other Pennatulacea, but also in those Gorgonida which possess a true axis. KOCH'S observations are conclusive that this epithelial layer, in the fixed Gorgonians, consists of invaginated ectoderm cells which secrete the axis as a cuticular structure. This "axis-epithelium" of the fixed Gorgonians is identical in structure with that of the Pennatulids, and the latter is believed by KOCH, though from analogy only, to be also ectodermic, its original connexion with the exterior having been lost.

In the face of such conflicting views as to the nature of the axis, it is impossible to determine its real relation to the peduncular septa and the *septum transversale*. Without definite knowledge on this point, it is clearly premature to frame any definite hypothesis as to the significance of the peduncular septum of *Renilla*, and the solution of this problem can only be found by studying the embryology of the axis-bearing Pennatulids.

§ 10. *Development of the mesenterial filaments.*

The mesenterial filaments are visible as soon as the larva becomes sufficiently transparent as dark granular thickenings on the edges of the septa at their upper portions where they join the œsophagus. They may be seen while the larva is still swimming, but their arrangement can be made out only after the larva has attached itself and the body has begun to elongate. It is then apparent that they vary in length and have a definite disposition. Those of the dorsal septa are very short indeed (fig. 177), or in some cases may not be visible at all when the others are well developed. They appear as knob-like prolongations of the lip of the œsophagus attached to edges of the dorsal septa. The dorso-lateral filaments (*d.l.f.*) are much longer, extending along the edges of the septa nearly to the buds (p^1.) which have now appeared at the point where the dorsal and dorso-lateral septa unite. The ventro-lateral filaments (*v.l.f.*) are still longer and extend down to the level of the buds or beyond them. The ventral filaments, finally, are very short, being intermediate in length between the dorsal and dorso-lateral filaments.

This grouping of the filaments is quite constant and exists at a very early stage. It is extremely difficult to determine whether these varying lengths represent the actual succession of the filaments since the latter are in their early stages closely contracted together and their arrangement cannot be made out. This grouping persists for a long time and the dorsal filaments remain permanently shorter than the others, and of different structure as Kölliker has observed. (The dorsal filaments are in many cases longer than the others, but this is, in *Renilla* at least, only apparent, and is due to the fact that they never become convoluted like those of the lateral and ventral septa.) All of the filaments except the dorsal pair increase rapidly in length and very soon become folded back and forth and variously convoluted (see figs. 183, 205). This is a result of the circumstance that the filaments increase in length much more rapidly than the septa which bear them, and they are necessarily therefore thrown into folds or "gathers."

The dorsal filaments grow backwards very slowly and are never thrown into transverse folds (see figs. 183, 204). They are less opaque than the other filaments, with a darker central line, and are of much less diameter than the others. These differences are permanent and persist in the adult. The dorsal filaments always remain in connexion with the œsophagus, and appear like long narrow prolongations of the latter down upon the edges of the septa. The other filaments, though at first extending quite up to the œsophagus, soon become more or less widely separated from the œsophagus, fading insensibly away a short distance below the lips of the latter.

In transverse sections the filaments appear as simple thickenings of the entoderm at the edges of the septa, which differ in appearance from the remaining entoderm of the septa only in being more granular. The supporting lamella may be traced out nearly to the middle of the thickening where it fades away and disappears.

The filaments appear to arise near the lips of the œsophagus, growing thence downwards along the septa. This suggests the possibility of ectodermic elements from the stomodæum entering into their composition, and I have made many longitudinal sections for the study of this point. Fig. 157 represents a longitudinal section through a larva of 100 hours (the mouth being fully formed) and the remains of the œsophageal plug (probably) being attached to a septum at *pl*. To the left is a mesenterial filament (*f*.) clearly outlined and well differentiated from the rest of the septum by its more intense colour and granular appearance. Above, the ectoderm of the stomodæum may be very clearly distinguished from the entoderm by its less granular appearance and different colour. Following the ectoderm of the stomodæum downwards, it passes insensibly into the entoderm of the filament without any indication of a limit between them. On the right side, however, the ectoderm is separated below by a faint rounded outline, below which the entoderm is slightly thickened and more granular. The large granular mass is possibly a filament but more probably the œsophageal plug. The same general features are shown in fig. 158, and the ectoderm at the left side of the stomodæum becomes entirely continuous below with the entoderm of a mesenterial filament (*f*.).

From these sections it might be concluded that the filaments are actually downgrowths from the stomodæum. In some cases, however, the filament appears to have at first no connexion with the œsophagus. This is shown for instance in fig. 159, where the filament (*f*.) on the left side ends in front by a definite rounded outline and has no connexion with the œsophagus. It is possible that this thickening on the septum is not really a filament but a part of the œsophageal plug. Nearly conclusive evidence is however afforded by the section shown in fig. 137. In this specimen there is a thickening on the edge of a septum (*f*.) which is probably the beginning of a mesenterial filament before the cavity of the œsophagus has broken through, and there is no possibility of any communication with the stomodæal ectoderm.

In *Leptogorgia* the filaments become visible shortly after the attachment of the larva. Two of them are much shorter than the others and are borne by a pair of septa which enclose one of the chambers at the angles of the elongated mouth; they are in all probability homologous with the dorsal pair of filaments in *Renilla*. The six other filaments are much longer and are equal to one another in length. This arrangement was maintained almost unchanged for seven weeks when the young polyps were killed.

Conclusions.

The mesenterial filaments are at first purely entodermic structures, formed as thickenings on the edges of the septa. After the absorption of the bottom of the œsophagus the ectoderm of the stomodæum becomes directly continuous with the entoderm of the edges of the septa and mesenterial filaments. Hence the possibility

certainly exists of the filaments or septa containing elements derived from the ectoderm. This must be borne in mind in considering the origin of the sexual elements which subsequently make their appearance in the walls of the dorso-lateral and ventro-lateral septa; for their derivation from the ectoderm is brought within the bounds of possibility. All writers agree that both ova and spermatozoa in the Anthozoa are derived from entoderm, and this has usually been regarded as beyond all question. The probabilities certainly appear to be very strongly in favour of this view, but it must, I think, be admitted that the possibility of an ectodermic origin for the sexual elements is not entirely excluded. [See Appendix.]

§ 11. *Changes of external form, appearance of the tentacles, and general histological changes.*

When the larva abandons its free-swimming life and settles upon the bottom it has a more or less elongated form, and the posterior part of the body is very extensible and changeable in shape. The ectoderm and entoderm have undergone little change. The entoderm cells are large and clear, with scanty coarse granules, and very distinct large oval nuclei. The ectoderm cells still retain their high columnar form, and have a finely granular contents, which stains slightly. The cells are planted on the lamella, and many of them extend through the entire thickness of the ectoderm. Besides the columnar form, there are other more or less rounded cells in the deeper layers of the ectoderm.

The body now elongates rapidly (figs. 176–178), and the ectoderm undergoes a great change. The columnar cells lose their form, become rounded, proliferate rapidly, and lose their connexion with the lamella. The outermost cells finally become flattened or fusiform, and form a thin layer covering the exterior of the body (see figs. 173–175). At the same time a considerable amount of clear gelatinous matter is formed, which sometimes entirely separates the cells from each other (figs. 160, 161), and forms the greater part of the ectoderm. In the deeper parts of the ectoderm appear rounded cells of various forms. Here and there are very large, deeply-stained, oval cells (fig. 166, *sp.*); others are nearly spherical, and groups of four deeply-stained cells are occasionally seen (fig. 166). Besides these, long fusiform cells may in some places be seen lying on the outer side of the lamella. These characters appear especially in the middle and posterior parts of the body. In the anterior region transitional forms may be seen, and at the extreme anterior end the columnar form is long retained.

The entoderm cells undergo meanwhile little change; they vary greatly in appearance according to the state of contraction of the body. During contraction they are of a high columnar form but when the body is fully extended they become much shortened or even flattened.

Leptogorgia presents the same general histological characters at this stage but the

ectoderm cells at the aboral end by which the larva attaches itself retain a high columnar form and very granular structure, and secrete a yellowish cement by which the young polyp is firmly attached. The entoderm is also much thickened at this point. This thickening of the layers is shown at *a*, in figs. 115 to 117. The cement substance is undoubtedly to be regarded as the first rudiment of the axis, which is therefore an ectodermic product. It is probable that budding takes place from the basal part of the young polyp so that the colony has at first the form of a flattened plate or encrustation covering the object to which it is attached by the cement secreted by the bases of the polyps. This may be inferred from the structure of the adult colony, but I did not succeed in observing the budding in young stages although the young polyps were kept for seven weeks in the aquarium. The individual shown in figs. 115 to 117 did not attach itself, and the thickening of the layers at the base was much greater than in those which became attached. Upon making a longitudinal section through this specimen, when seven weeks old, the dark mass, *a*, was found to contain a solid yellow horny mass composed of a substance quite like the cement by which other individuals were attached. The basal part of the wall of the body seems to have been invaginated and the cement then secreted in the cavity thus formed. The polyp therefore appeared to have an internal axis, but this must be regarded as an unusual condition which probably occurs only when the larva fails to attach itself.

The tentacles, in both genera, appear soon after the attachment of the larva as conical outgrowths from the anterior ends of the radial chambers (figs. 115 and 176). I have not observed the least difference in the time of their appearance though I have observed them in every stage of development and in many different individuals. In this respect, as in the formation of the septa, the development of the Alcyonaria is more abbreviated than that of the Zoantharia; for in many representatives of the latter group the tentacles, like the septa, develop in regular sequence.

The tentacles are at first quite simple, with no indication of pinnæ. The latter soon make their appearance along the sides of the tentacles, a new pair being formed, roughly speaking, every day. The new pinnæ are formed near the base of the tentacle and are carried outwards by the longitudinal growth of the latter. The formation of pinnæ ceases after about ten to twelve pairs have appeared and the growth of the tentacles is arrested. The pinnæ are somewhat irregularly disposed and the paired arrangement often disappears towards the tip of the tentacle. Those in the middle of the tentacle are always longer than the basal or apical ones. The pinnæ are formed as simple diverticula from the tentacle and consist accordingly of a layer of ectoderm and entoderm separated by the lamella and enclosing a prolongation from the cavity of the tentacle. The tips of the tentacles and pinnæ are often slightly swollen from the accumulation of minute thread-cells at these points.

§ 12. *Development of the spicules and calyx-teeth.*

The spicules of *Renilla*, as EISEN observed, are of two different forms, and I have found these to have an entirely different origin. The large elongated spicules which give the colony its beautiful purple colour and stiffen its walls are produced entirely by the ectoderm. On the other hand the small transparent oval spicules, which occur in small numbers only, are developed in the entoderm alone.

The former make their appearance soon after the attachment of the larva on each side of the middle region of the body near the first pair of buds. They have the appearance of delicate transparent rod-like bodies which are at first quite colourless. They increase slowly in number, extending backward along the line of the peduncular septum on each side. It is only when the formation of the colony is well advanced that they acquire a purple colour and begin to extend forwards towards the oral extremity and upwards and downwards around the body. They gradually extend over the whole area of the body which therefore acquires a delicate purple tint, except towards the tip of the peduncle which remains white. The spicules become very scanty or quite disappear towards the anterior extremity and assume a peculiar arrangement at their upper limit. In each compartment some distance behind the bases of the tentacles they arrange themselves in lines radiating backward and sidewise from a small central area which ultimately forms the tip of a calyx-tooth (fig. 185, *cx.*). At the same time this region becomes elevated so as to form a low conical prominence which in later stages gradually grows out into a hollow pointed diverticulum from the chamber, its walls being stiffened by long spicules; this is a calyx-tooth. When the crown of tentacles is retracted the tooth lies at the anterior end and forms a hard pointed prominence projecting forwards. Calyx-teeth appear on all of the chambers except the ventral one where the formation of a tooth is a rare exception.

In transverse sections the needle-shaped spicules are found to lie in the lower layers of the ectoderm outside the lamella, and a study of the smallest spicules shows that they are formed in the interior of rounded cells lying in the ectoderm. It is difficult to demonstrate the spicule-cells, even in the earliest stages of the spicules, and I have never seen them with certainty after the spicules have attained any considerable size. They cannot be isolated by teasing, and when *in situ* it is difficult to distinguish them from the surrounding cells. By staining the tissues deeply with eosin the bodies of the cells may occasionally be clearly distinguished. Figs. 171^e to 171^j show different forms of the cells containing very young spicules. In some of the cells nuclei appear; in others they are invisible. The calcareous matter first appears as an irregular elongated mass in the protoplasm of the cell and shows to the eye no trace of crystalline structure. As a rule there is only a single concretion in a cell, but the spicules are occasionally formed from two centres, as in fig. 171^e. As the spicule increases in size the enclosing layer of protoplasm becomes very thin and I have never

been able to demonstrate it in spicules of one-fourth the full size. The largest spicule figured (*g*.) is not more than one-eighth the length of a fully formed spicule.

The entodermic spicules (figs. 172[a] to 172[e]) make their appearance at a much earlier period than those of the ectoderm. They first appear in the lateral portions of the peduncular septum as oval, highly refractive bodies, which are plainly visible from the exterior (fig. 181). They become in time very numerous and are arranged in an irregular longitudinal band on each side of the septum. They appear also in the entoderm of the lateral walls of the body and are especially numerous near the posterior end. They become easily detached from their points of origin and may often be seen suspended in the fluid which circulates in the cavities of the young polyp. Most of the spicules of the peduncular septum are formed in its two outer layers, but it often happens that a few are developed in the axial cells and when the latter atrophy are left embedded in the lamella (see p. 766).

The entodermic spicules also are formed in the interior of cells which may much more readily be demonstrated than the ectodermic spicule-cells. The cells, as shown in fig. 172, are variable in form and usually contain distinct nuclei. The calcareous matter is first deposited in the form of very minute rounded nodules which, as in the case of the ectoderm spicules, may be clearly brought into view by examination with polarised light. Examined by ordinary transmitted light they appear in their earliest stages as transparent, scarcely visible bodies: or they may be quite invisible. If, however, they be examined with the polariser, and the upper prism be rotated, they come into view with the greatest clearness; and by a proper adjustment of the prisms both the cell and the calcareous nodules come clearly into view. The spicule-cells may contain only one nodule, or two or three may be present. In the latter case each nodule appears in some cases to give rise to an independent spicule. In other cases spicules may be seen more or less closely united in groups of two, three, or four, and it is probable that each such group is developed within a single cell. The form of the nodules varies exceedingly, being spherical, oval, or irregularly angular. A not uncommon appearance is shown in fig. 172[a]. The spicule has an oval form and its substance refracts the light in such a way as to produce two darker lozenge-shaped areas at the ends. The fully formed spicules are usually of a smoothly rounded oval form but are in many cases obscurely angular at the ends (see figs. 172[e]). This is not definite enough, however, to admit of comparison with inorganic crystals.

If the spicules be treated with dilute acid, the calcareous matter is dissolved with effervescence, leaving a nearly transparent organic basis which accurately retains the form of the spicules. In some cases, at least, their organic basis is formed before the calcareous matter is deposited. I have sometimes seen cells resembling the spicule-cells, and containing clear bodies quite similar to the calcareous nodules, but destitute of calcareous matter.

In order to determine the molecular structure of the spicules, I submitted a number of them to Professor B. K. Emerson, the well-known mineralogist of Amherst

College, for examination with the polariscope. He kindly undertook to examine them, and the following statement of his results is quoted verbatim:—

"I find the smaller spicules to polarise perfectly and very brightly, and if the spicules are a carbonate, it is probably aragonite rather than calcite, because of the bright colour it affords.

"Each spicule is made up of a core of crystalline material surrounded by a thin layer of non-polarising matter, and this by an outer layer, slightly thicker, and also of equal thickness, which polarises as does the core.

"The crystalline axes uniformly run parallel to the long and short diagonals, as in the sketch, so that the core is a crystal probably of the rhombic system, and the outer layer is controlled in its position by this core and has parallel axes with it.

"The larger spicules I can best explain by saying that for a moment, on examining the slides, I supposed the small ones to be cross sections of the former (larger) ones. They are like bones filled with marrow under the microscope, the bone and the marrow representing the core and the outer layer of the small ones, and these being separated by an amorphous (in one case there were two amorphous layers) layer. In this case, the long axis of the spicule is a crystallographic axis. And bone and marrow are *orientirt* alike."

From this, the very interesting fact appears that the spicules are formed by a true process of crystallisation, though the form and structure of the crystals are modified, probably by reason of their deposition in an organic viscous medium. This point, as noted below, is one of much theoretical interest.

In *Leptogorgia* the characteristic spicules appear in the ectoderm soon after the attachment of the larva. They are quite irregularly distributed, and extend up into the bases of the tentacles. No entodermic spicules were observed.

Review.

My observations on the development of the spicules are in accord with those of KOWALEVSKY on the spicules of *Sympodium* (Zool. Anzeiger, No. 38, 1879), and as KOWALEVSKY points out, the process is quite similar to the formation of spicules in the mesoderm cells of sponges observed by SCHULTZE and METSCHNIKOFF. Their mode of development strongly recalls the formation of inorganic crystals in the interior of vegetable cells, and possibly indicates the origin of the spicular skeleton. This

question presents serious difficulties under the theory of natural selection, for it is impossible to see how the occasional appearance of minute calcareous nodules in the tissues can originally have been of any use to the organism.

Everyone is familiar with the formation of crystals of lime salts in the interior of vegetable cells, where they perform no function as supporting organs, and are apparently mere by-products of the activity of the protoplasm. In this respect the entodermic spicules of *Renilla* resemble the deposits in many vegetable cells; for they are of no use to the colony as supporting organs, and unless we consider their present condition as having been acquired through degeneration, they must originally have been developed without reference to such a function. From the analogy of the deposits in vegetable cells, and in the entoderm cells of *Renilla*, it seems not improbable that the ectodermic spicules of *Renilla* had originally no function as supporting organs, having been formed simply as by-products of the activity of the protoplasm under peculiar conditions, such, for instance, as a superabundance of lime salts in the water. If, however, calcareous nodules once made their appearance in any considerable quantity in the tissues, they might serve as supporting organs, and be developed through natural selection to almost any extent. They might thus attain the great size and functional importance of the ectodermic spicules of *Renilla* or other Pennatulids, or by agglutination come to form a compact skeleton as in *Tubipora*.

It is remarkable to find so wide a difference between the skeletons of Alcyonaria and Zoantharia, as must exist if KOCH'S recent conclusions as to the skeleton of *Asteroides calycularis* are well founded;* and it seems probable that the skeleton has been quite independently acquired in the two groups. The present considerations will, of course, apply to the Alcyonarian skeleton only.

§ 13. *Development of the muscular system.*

The larva of three days is very changeable in form (figs. 104, 105), showing that contractile elements have made their appearance; and careful examination of specimens rendered transparent by reagents reveals the presence of numerous short delicate unstriated muscle-fibres underlying the ectoderm. These are found to have a definite and constant arrangement, which will be described before considering the histology of the tissue.

a. Distribution.

The muscle-fibres are from the first arranged in two systems, viz.: a layer of longitudinal fibres, and a layer of circular fibres, which ultimately come to lie outside the former. The circular fibres first appear in the posterior half of the body in a broad

* Mittheilungen aus der Zool. Station zu Neapel, Band iii., Heft iii., 1882, pp. 284–292.

sheet which nearly encircles the body, but is interrupted at certain points where the longitudinal fibres are situated. As seen in surface view (figs. 160, 161 *c.m.*) they appear as delicate transparent fibres which are quite disconnected from one another. The sheet of circular fibres extends at first no further forwards than the first pair of buds; but as development proceeds the fibres extend forwards to the oral extremity. In the tentacles they seem never to be developed.

The longitudinal fibres differ from the circular in being at first arranged in definite tracts. These correspond in part with the septa, a narrow band of fibres following the line of attachment of each of the radial septa, and of the peduncular septum on each side of the body; these may be termed the septal tracts. Besides these there are two median tracts extending forwards, above and below, from the posterior extremity of the body. The dorsal median tract extends forwards nearly to the first pair of buds and there terminates. The ventral median tract bifurcates at its anterior extremity, and the two branches become continuous with the tracts of the ventral septa (see fig. 176 and p. 765). This arrangement of the longitudinal muscles is strongly bilateral, the median plane corresponding with the dorso-ventral axis of the body. From these primitive tracts the longitudinal fibres gradually extend laterally until they form an unbroken sheet lying within the circular fibres. They also extend forwards into the tentacles, and out towards their tips.

In transverse sections the longitudinal fibres appear as small dark spots lying in the basal part of the entoderm just within, and in contact with the supporting lamella. The entoderm cells covering the median tracts always show a fan-shaped arrangement, which is especially marked in younger stages, while the tract is still very narrow, as shown in fig. 162 (dorsal tract). Fig. 164 represents the ventral tract of a young specimen, and fig. 163 the same tract of an older individual.

The septal tracts (fig. 165) are divided into two parts by the lamella of the septum. In early stages these two parts lie at the base of the septum; but as development proceeds the fibres on the *ventral* side gradually extend out into the septum, until at length they cover a broad tract on the ventral face of the lamella. They also extend for some distance out upon the ventral face of the peduncular septum (fig. 167). (The presence of longitudinal muscles in the lateral portions of the peduncular septum is mentioned by Kölliker, 'Pennatuliden,' p. 274.) These muscles form the retractors of the polyp, which have therefore the arrangement characteristic of all the Alcyonarian polyps which have thus far been examined. (*Cf.* Kölliker, Eisen, Lindahl, Moseley, and Haacke.)

The circular muscles can scarcely be seen in transverse sections, but are here and there visible, as in fig. 169. In longitudinal sections they are plainly visible (fig. 168) as a series of dark spots within the supporting lamella. They are somewhat irregularly placed, and are not grouped in definite tracts.

b. Histology.

By macerating the tissues in HERTWIGS' mixture of osmic and acetic acids (see p. 728) the entodermic elements can be teased apart, and the muscle-cells completely isolated. We find thus that each muscle-fibre is developed from the base of an entoderm cell, the fibre and cell together constituting an "epithelio-muscular" cell or—to adopt the more convenient term proposed by CLAUS—a myoblast.

The myoblasts are of exceedingly diverse forms, as illustrated by the series of figures (170^a to 170^e). There is great variation in the length of the fibre, depending apparently on the age of the fibre, since the shorter ones are often no thicker than the longer.

The fibres taper towards both ends and are sometimes thrown into transverse folds. They consist of a homogeneous highly refractive substance which differs entirely from the body of the cell. The latter is composed of a granular substance, and contains a distinct rounded nucleus. As to the form of the cell, every gradation may be observed between a regular columnar cell planted on the fibre (fig. 170^d) and a slight accumulation of protoplasm surrounding a nucleus, which is closely applied to the side of the fibre (fig. 170^e). In all of the forms a delicate layer of granular protoplasm often extends for a considerable distance along the fibre (see figs. 170$^{b, c, e}$).

From these appearances I conclude that the body of the cell always extends at first to the surface of the entoderm, the myoblast being at this stage a typical "epithelio-muscular" cell. As the fibre increases in size the body of the cell sinks into the entoderm and diminishes in size, the myoblast then becoming an "intra-epithelial" muscular cell (HERTWIGS). Finally, the myoblast is wholly buried in the entoderm, the cell-body dwindles away and a "sub-epithelial" cell results—*i.e.*, an ordinary nucleated muscle-fibre. This course of development is, however, only inferred from the perfect series of forms shown among the myoblasts, since the outlines of the cells cannot be distinguished in the sections with sufficient clearness to follow their development.

The fibres of both layers are at first arranged in simple flat sheets. Later, the lamella is thrown into folds, so that both systems of muscles assume a more or less arborescent form in sections. The foldings take place in a very peculiar manner, such that those of the longitudinal layer alone are visible in transverse sections, and, *mutatis mutandis*, those of the circular layer in longitudinal sections. I have not followed in detail the development of these folds, since it has been very thoroughly studied by the HERTWIG Brothers in the Actiniæ.

Review.

Both systems of muscles, circular and longitudinal, are formed in the entoderm alone, and an ectodermic musculature is entirely wanting, with the possible exception of some of the muscles of the tentacles. No other case of a purely entodermic muscu-

lature, so far as I am aware, is known to exist, though in most of the Actiniæ the ectodermal muscles are very feebly developed, as JOURDAN and the Brothers HERTWIG have shown. This result can, however, hardly occasion surprise, in view of the astonishing amount of variation in the musculature of polyps. KOWALEVSKY states that the longitudinal muscles of *Alcyonium* are of entodermic origin, but refers the circular muscles doubtfully to the ectoderm. Beyond these, observations on the embryonic development of the muscles in Alcyonaria are wanting.

In their mode of development the muscle-fibres agree with other Cœlenterata with exception of the Ctenophora. They are developed in the form of epithelio-muscular cells or myoblasts, which have the same form and structure as those of other Anthozoa, as described especially by the Brothers HERTWIG and by JOURDAN. The myoblasts do not, however, retain this form permanently, as is the case with many polyps. The cell-bodies become reduced to a small quantity of protoplasm enclosing a nucleus, and the myoblast is situated beneath the epithelial layer as in the medusæ (HERTWIGS), some hydroids (KOROTNEFF, CIAMICIAN), and a number of polyps (HERTWIGS, JOURDAN). It is, however, possible that some of the epithelio-muscular cells may retain this form permanently.

III.

DEVELOPMENT OF THE COLONY.

The primary polyp of *Renilla*, produced by sexual reproduction from the egg, begins at a very early age to produce secondary polyps by budding, and thus builds up a community or colony of individuals organically united together. Although this process is a very common one among the Anthozoa, and is all but universal among the Alcyonaria, it possesses a special interest in the case of *Renilla*, on account of the very early period of life at which the power of asexual reproduction is developed, and more especially from the remarkably definite and constant structural relations existing between the members of the community.

§ 14. *Development and functions of the first pair of sexual polyps.*

When the larva is no more than seventy-two hours old, and is still actively swimming through the water, a pair of buds make their appearance on the dorsal side, just above the point where the dorsal and dorso-lateral septa join each other and the peduncular septum. This position of the buds is entirely constant, and I have never seen the least variation from it in the many hundreds of specimens examined.

The buds, as shown at p^1. in figs. 103, 104, appear as slight rounded elevations, with darker centres and without visible septa or mouth-openings. Upon making a longitudinal section through the bud at this stage (*i.e.*, a section transverse to the axial polyp) we find that the darker centre is produced by an ingrowth of ectoderm

(fig. 173, *st.*) which forms the first rudiment of the œsophagus, and is therefore a stomodæum. The lamella (*sl.*) is pushed inwards for some distance so as to form a kind of pouch, filled with a solid mass of ectoderm. The lamella at the bottom of the stomodæum then becomes perforated, so that the ectoderm becomes continuous with the entoderm, though there is still no cavity in the œsophagus. The process is fundamentally like the formation of the stomodæum in the axial polyp, but the mouth-opening is differently formed. The cavity of the œsophagus appears as a funnel-shaped depression at the inner end of the stomodæum opening within into the gastric cavity of the axial polyp and terminating outwardly in the solid plug of ectodermic tissue which forms the stomodæum. The cells of this plug are small and rounded, without definite arrangement. Farther inwards the ectoderm cells assume an irregularly columnar arrangement on either side of the cavity, and at the inner end of the stomodæum become definitely columnar and graduate insensibly into the entoderm cells around the lips of the œsophagus.

The cavity of the œsophagus soon breaks through to the exterior, forming a small oval opening, the mouth, which gradually becomes elongated in the dorso-ventral plane until it has the form of a long cleft. The cells of the stomodæum become at the same time of a high columnar form, and cilia make their appearance at the inner ends of those on the ventral side. By the action of these cilia strong currents are drawn into the colony through the mouths of the buds which are held widely open. These currents may be readily shewn by adding finely-powdered carmine to the water, when the particles may be seen to be sucked with force into the mouths of the buds. In this manner large quantities of water are sucked into the cavity of the axial polyp, whose body may thus become greatly distended. When a sufficient amount of water has been taken in, the mouths of the buds are tightly closed, and the water is thus retained. The water thus taken in is kept in active circulation by means of the cilia which cover the entoderm. The currents, which are rendered plainly visible by the particles suspended in the fluid, follow a definite course. In the upper chamber of the peduncle the current sets always backwards, and the fluid flows thence into the lower chamber through the openings along the sides, and at the posterior end of the peduncular septum. In the lower chamber the current flows forwards into the anterior part of the gastric cavity.

It is by means of the fluid contained in the gastric cavity that the young polyp is enabled to effect the active creeping movements which it now performs. The *modus operandi* is as follows. The anterior part of the body being well distended, an active peristaltic contraction of the circular muscles takes place and the fluid is thus forced backwards into the posterior region (which may now be termed the peduncle). The latter consequently becomes much elongated, somewhat as the ambulacral "foot" of an Echinoderm is protruded, and the body is pushed forwards a short distance. The circular muscles then relax and the longitudinal ones contract in such a manner as to pull the posterior region forwards towards the anterior part which adheres to the

bottom. By the constant repetition of this process the whole organism moves slowly forwards. The creeping movements are very irregular, since the action of the muscles is not uniform. The longitudinal muscles frequently contract more on one side than on the other, so that the body sways and twists about from side to side, often turning completely over and undergoing all kinds of contortions. Nevertheless the organism often creeps for a considerable distance and may even crawl up the perpendicular sides of a glass vessel. The same power of active movement is possessed by the adult colony, and the conditions under which the organism lives are obviously such as to render this power of vital importance to the creature. Living as it does on shifting beds of sand, the colony would be buried and smothered were it not for this power of creeping. If, however, a *Renilla* colony be covered with sand in the aquarium, it soon works its way to the surface and the polyps are enabled to expand in the water.

In the vital necessity of the power of movement lies no doubt the explanation of the very early appearance of the buds. If the young polyp, upon abandoning its free-swimming life and settling in the sand, possessed no means of taking in water and thus of creeping, it would be very apt to be smothered in the shifting sand. By the very early appearance of the buds the young polyp is enabled to imbibe water and to creep as soon as the sedentary life is assumed, and is thereby preserved from destruction.

This view receives a strong confirmation upon comparing *Leptogorgia* with *Renilla* in this respect. The former does not possess the power of creeping but attaches itself at an early age to solid objects in situations where it is not likely to be buried. Precisely as we should expect under the foregoing view, the buds of *Leptogorgia* do not appear at an early period. In my specimens, in fact, they had not made their appearance at the end of nearly two months (!), whereas in *Renilla* they appear at the end of three days.

As the buds become older and more fully developed they gradually cease to perform the function of imbibing water. It is however assumed by younger buds and is in turn lost by the latter as they become older. Throughout the entire life of the organism this function is performed by the sexual polyps in their early stages. The function is lost, so far as I have observed, as the bud becomes mature and is adapted to perform the functions of nutrition and reproduction. This may readily be demonstrated by placing a contracted colony in a vessel of water containing finely divided carmine. The water is forcibly sucked in through the mouths of all of the young marginal buds, but never through the adult polyps. This function is performed by the zooids during their entire existence; so that the latter structures are physiologically identical with the young sexual polyps (see § 21).

As may be seen in fig. 173, the bud lies at first almost entirely inside the primary polyp, projecting inwards from the body wall and forming only a very slight prominence on the exterior. As development proceeds the bud is pushed outwards so as to form an obtusely conical elevation on the exterior (fig. 178, p^1.). At the same time the entoderm grows downwards from the tip of the bud in eight radiating plates (fig.

178^{d}) stretching between the wall of the œsophagus and the lateral wall of the bud. These are the septa. They have the same structure as in the young primary polyp, consisting of two layers of entoderm cells separated by a delicate supporting lamella which joins that of the body-wall. As the septa are formed the outer wall of the bud becomes divided into eight lobes (fig. 184^{a}) which correspond with the eight chambers of the body. As the bud grows outwards (*cf.* fig. 205,) the septa grows inwards (i.e., downwards toward the axial polyp) so that their lower extremities remain at about the level of the body-wall of the primary polyp.

The septa when first formed stand at nearly equal intervals from each other, though those on the dorsal side are often a little more crowded than the others. As the bud develops farther the septa assume a definite arrangement as shown in fig. 184^{a}. The ventral pair approach more closely so that the ventral chamber, which is opposite one end of the elongated mouth, becomes distinctly narrower than the two adjoining ventro-lateral chambers. As shown by the later development, the narrow ventral chamber is homologous with the ventral chamber of the axial polyp and we are thus enabled to determine the orientation of the young polyp. We find that the dorso-ventral axis of the bud has a constant position with reference to the primary polyp, which is shown in fig. 184^{a}; *a–p* represents the long axis of the primary polyp, and *d–v* the dorso-ventral axis of the bud. The latter cuts the former nearly at a right angle, but is always inclined slightly forwards (*a* represents the anterior extremity of the axial polyp).

I will add a brief account of the habits of the young colony at this stage.

If the creature be left to itself it gradually comes to a state of rest, burying the peduncle in the sand. The body always assumes nearly the same position, the dorsal side (as determined by the interior structure) being held upwards and the buds extending horizontally on either side. The anterior part of the main polyp, with its crown of tentacles, is directed obliquely upwards and forwards. This position is maintained throughout all the following stages, and this is, I believe, a fact of the greatest importance which stands in causal connexion with the bilateral symmetry of the organism.

The tentacles of the axial polyp may at this stage be entirely retracted into the anterior part of the body. This is effected by the invagination of the oral end of the body, the tentacles being at the same time strongly contracted. When fully expanded they are held nearly horizontally with the outer portion curving gently backwards. When the polyp is hungry the tentacles are moved actively back and forth, somewhat after the fashion of a *Synapta*, but without regularity. If supplied with food, such as Gasteropod veligers, the tentacles close eagerly upon it, and it is held for some time closely clasped by them. They are then taken into the œsophagus and passed in a bolus down to its lower portion where they remain for some time, the lower opening of the œsophagus remaining tightly closed. The

bolus is at length suddenly passed into the stomach and retained during digestion in its upper portion. I was unable to discover any indication of intra-cellular digestion. The contents of the veliger shells were dissolved out and were then circulated through the gastric cavity in the form of oil globules. The empty shells were finally ejected through the œsophagus by a reversed peristaltic action.

In *Leptogorgia*, which was fed with oyster larvæ, the process was slightly different. The larvæ were passed into the œsophagus until a large bolus was accumulated at the lower end. The bolus was then passed into the stomach and closely clasped by the short mesenterial filaments. It was thus held for two or three hours, and its remains were finally ejected through the mouth. This seems to indicate that the filaments are intimately concerned in the process of digestion; but, as before, I could not determine the mode of action of the cells.

This observation is interesting, taken in connexion with KRUKENBERG's physiological studies upon the nature of the filaments in the Actiniæ.* From experiments on artificial digestion he is led to conclude that the mesenterial filaments are mainly or entirely concerned in the act of digestion—so far, at least, as proteid matters are concerned—and my observations seem to point in the same direction.

§ 15. *Arrangement and succession of the sexual polyps.*

I have not succeeded in raising the young colonies in the aquarium beyond the stage shown in fig. 178, and my observations on the later stages were made from specimens procured in the sand, which were found in every stage of development. Hence I cannot give the rate of development, since the young colonies develop very slowly or not at all when kept in aquaria. Large numbers of them were examined and the succession of the buds was found to be nearly constant in early stages though somewhat variable in later ones.

The buds develop always symmetrically in pairs with wonderful regularity, as the accompanying series of figures will show. The appearance of the first pair has already been described.

The second pair invariably appear just behind the first (fig. 182, p^2.), and their mode of development is quite like that of the first pair. As soon as the dorso-ventral axis can be distinguished, they are found to be placed like those of the first pair, though the obliquity is less marked, and the axis of the buds often form a right angle with the long axis of the primary polyp. The second pair are at first quite disconnected from the first pair, but soon fuse to some extent with them, the buds being separated by a thin partition wall which terminates by a free edge below (fig. 204, *c*.). The third pair are formed some time after the second, a short distance in front of and obliquely below the first. As before, they are at first quite separate from the other buds, but soon fuse with the first pair (see figs. 204 to 207). The

* Vergleichend-physiologische Studien an den Küsten der Adria, Erste Abtheilung, 1880.

fourth pair (Fig. 185, p^4.) arise in front of and slightly below the third in the same manner as the other buds.

Up to this point the order of succession is almost invariable. The sequence in the appearance of the remaining buds is subject to considerable variation, though their position is definite and constant. They make their appearance in the angles between the buds already formed, and in the angles between these and the primary polyp; this will be rendered clear by an inspection of figs. 186 to 188.

In fig. 185 a fifth pair (p^5.) have appeared between the first and second. In fig. 186 two additional pairs (p^6. and p^7.) have appeared; one pair (p^6.) are placed in the posterior angles between p^2. and the primary polyp, and the other (p^7.) are between p^1. and p^5.

Fig. 187 is a still older colony in which five new pairs, besides the seven of fig. 186, have appeared.

Of these new pairs p^{12}. are placed in front of the entire series, while the remaining four (p^{11}., p^{10}., p^9., and p^8.) are placed in the angles between p^5.–p^4., p^1.–p^5, p^5.–p^2., and p^3.–p^6., respectively.

Fig. 188 is a still later stage with the tentacles retracted.

The buds are designated as before. Only one additional pair has appeared (p^{13}.), but those of the last stage have greatly increased in size, as may be seen by comparing the corresponding buds marked p^{10}. in the two figures.

The colony has now assumed the form of a flattened disc, with polyps in various stages of growth situated all around the edge. This form results from the circumstance that the secondary polyps grow out laterally away from the primary polyps, and the younger polyps borne in their angles are thus carried further and further away from the centre of the group. The longitudinal axes of the secondary polyps radiate in every direction from the central point. The posterior part of the axial polyp (*ped.*) may now be recognised as the peduncle of the colony.

It has already been noted that the third bud lies a little below the level of the first, and the fourth a little below the third. The buds are therefore arranged on each side in an oblique line, extending forwards and downwards. This line is continued by succeeding buds so that the anterior buds finally come to lie partly on the lower side of the axial polyp, as at p^{13}. in fig. 188. The two lines of buds finally meet one another at the ventral side of the axial polyp. The latter meanwhile bends gradually upwards so that the two lines of buds are kept nearly horizontal, and when they meet are situated at the anterior edge of the disc, and not at its lower side. The axial polyp is thus cut off entirely from the edge, and now rises from the upper side of the disc. This process will be rendered clear by an inspection of fig. 189, where *ax.* designates the axial polyp, and p^{12}., p^{13}., the foremost pair of lateral buds which have united behind the axial polyp at the point *x*. In the angle between p^{12}., p^{12}. has appeared a median bud which completes the outline of the disc in front.

The portion of the axial cell which is included in the disc, forms the "polyp-cell"

and its free portion is what is usually termed the polyp. The latter may be entirely invaginated into the former by the action of the longitudinal muscles of the septa. The calyx-teeth, which have meanwhile increased greatly in length, are situated just at the upper surface of the disc, and when the polyp is retracted they radiate from the opening of the cell (see fig. 189).

The foregoing account of the enclosure of the axial polyp will apply equally well to the secondary polyps. On account of the continual appearance of young buds in the angles between older ones, each of the latter is bordered by younger polyps on each side. The latter gradually extend downwards, and finally meet behind the older polyp which at the same time bends upwards, and thus becomes enclosed within the disc. This is shown in fig. 188, where p^7. and p^{10}. are already extending behind p^1.

As mentioned at p. 789, the ventral compartment of the polyp never has a calyx-tooth, a fact which is rendered conspicuous when the polyps are retracted (see fig. 189). When the polyp turns upwards and is enclosed in the disc, the ventral chamber necessarily comes to be situated on the outer side of the polyp or away from the centre of the group.

By the union of the lateral lines of buds the outline of the disc is completed at front, and the marginal buds now form an unbroken series from one side to the other behind the axial polyp. At the posterior part of the disc, however, the outline is never completed and a permanent sinus remains in which the peduncle is attached. This is due to the cessation of the formation of lateral buds in the posterior angle after three or four buds have been formed (see fig. 189).

§ 16. *Formation of organs in the secondary polyps.*

The early development of the bud, including the formation of the œsophagus and septa, has already been described; but we have still to consider the development of organs in later stages. The bud agrees in the main with the primary polyp, but there are certain important differences in the sequence of development of certain organs.

a. Development of the calyx-teeth.

As the bud grows outwards the outer ends of the chambers grow out into obtusely conical projections, which ultimately form the calyx-teeth, though they are at first closely similar to tentacles. As observed by Köllikeр and Eisen, they are formed in definite sequence, and I can in the main confirm the accounts of these authors. This sequence cannot be observed in the appearance of the calyx-teeth of the primary polyp, and is only obscurely shown in the buds which are first formed. As the colony increases in size, however, the sequence becomes very marked, especially in the posterior parts of the disc where the calyx-teeth are usually longer than elsewhere.

Figs. 190 to 193 illustrate the most usual succession of the teeth. The first to develop are those of the ventro-lateral chambers (fig. 190). These are often enormously elongated, especially in the posterior parts of the disc, and they remain for a long time distinctly longer than the others, as may be seen in fig. 193. After a considerable interval they are followed by the calyx-tooth of the dorsal chamber (fig. 191). The lateral teeth appear nearly simultaneously; but so far as I have observed, the median-lateral teeth usually precede somewhat the dorso-lateral. This is sometimes quite decided (fig. 192); but in a few cases the dorso-lateral teeth are first to appear. According to KÖLLIKER this is the rule, and he states that when five teeth are present, the missing teeth are always those of the median-lateral chambers. The ventral chamber very rarely develops a tooth. In younger buds, when all of the teeth are formed, they usually increase pretty regularly in length from above downwards, and this gradation is more marked usually in posterior parts of the disc. In later stages, the difference gradually becomes less, until the teeth are of nearly equal length. In the rare cases of the appearance of a ventral tooth this is always smaller than the others. The calyx-teeth vary greatly in length in different colonies. We note, finally, that the calyx-teeth are usually all formed before the tentacles appear, whereas the reverse is true of the primary polyp.

It is surprising to find this regular succession in the appearance of the calyx-teeth, which must be structures much younger, phylogenetically, than the tentacles. It may perhaps depend upon the circumstance that the polyps are in early stages placed side by side, so that the upper and lower calyx-teeth are more directly exposed to the environment. This does not, however, account for the absence of a tooth on the ventral chamber, and in our ignorance of the functions of the teeth in early stages, it is useless to speculate on the matter. In the mature bud the teeth probably serve as an armature for the mouths of the polyp-cells, since they are then stiffened with spicules and must form an effective defence. They can hardly perform such an office, however, in the young buds and in the zooids, though their early and ample development in both these cases indicates that they must perform some function. The very brilliant and beautiful phosphorescence of the colony appears to have its principal seat in the calyx-teeth of the young buds; but this can hardly throw any light upon their function.

Whatever be their function, the sequence in the development of the calyx-teeth seems to stand in no relation with the definite succession of the tentacles in some Zoantharia, but is dependent upon some special unknown conditions peculiar to the *Renilla* colony.

b. Development of the tentacles.

The formation of the tentacles agrees entirely with that of the tentacles of the primary polyp, and calls for no special remark. They make their appearance simultaneously, after the formation of the calyx-teeth, as conical outgrowths of the

compartments between the mouth and the calyx-teeth. They are at first simple, but soon become pinnate, the pinnæ developing somewhat irregularly in pairs at the bases of the tentacles.

c. Development of the mesenterial filaments.

The mesenterial filaments are formed in essentially the same manner as in the primary polyp, appearing as thickenings on the edges of the septa. They differ however in one striking feature from the filaments of the primary polyp, viz.: in the order of their appearance. The dorsal filaments in the latter are last to appear and slowest in development, whereas in the buds they are in many cases first to appear, and in all cases develop at first more rapidly than the other six. This agrees entirely with KÖLLIKER'S observations on the development of the secondary polyps in *Halisceptrum* ('Pennatuliden,' p. 161) in which the dorsal filaments are well formed before a trace of the other six can be made out.

This remarkable contrast between the development of the filaments of the primary and secondary polyps shows clearly that in searching for the relations between the various groups of polyps, as indicated by their embryology, we are not justified in comparing the egg-development of one form with the bud-development of another, or in taking the structure of the bud as any necessary indication of the succession of the parts in the egg-embryo. That the importance of this principle has been unconsciously disregarded will, I think, be clear from the following citations.

MOSELEY writes in his admirable paper on *Heliopora* and *Sarcophyton* (Phil. Trans. Vol. 166, 1876, p. 121): "It seems extremely difficult to reconcile the extraordinary succession of the mesenteries in the development of the Zoantharians, discovered by LACAZE-DUTHIERS, with the facts presented by Alcyonarians. Did the development of the eight mesenteries of Alcyonaria correspond with that of the first eight mesenteries formed in Actiniadæ, the first mesenteries formed would be either the lateral dorsal or lateral ventral; but these are those which are most rudimentary in the zooids of *Sarcophyton*. Moreover the mesenterial filaments of the two lateral pairs of septa are in the development of Actiniadæ the first to appear, and not the dorsal, which are longest in the Alcyonarian polyps and most persistent in the zooids. Apparently, however, development in Alcyonarians follows a different course."

These words seem clearly to imply that the greater length of the dorsal filaments and their persistence in the zooids indicates their earlier development in the embryo.

KÖLLIKER states explicitly ('Pennatuliden,' p. 427): "Die Septa und Septula sind Falten des Entoderm und entstehen wahrscheinlich alle zugleich (ich), dagegen bilden sich in erster Linie nur an zweien derselben Verdickungen des Entoderma (Mesenterialfilamente) und später erst treten solche auch an den andern 6 Septa gleichzeitig auf." At p. 434, he even extends this statement so as to apply to the entire group of Alcyonaria: "Bei den Alcyonarien treten nun allerdings auch *zwei* Mesenterial-

filamente früher als die anderen auf, allein diese stehen *dicht beisammen*, und bilden sich nach allem, was wir wissen, alle acht Septa auf einmal."

Nevertheless, in *Renilla* at least, the exact reverse of what is indicated by the passages cited is actually the case; and the presumption is that the same holds true in *Sarcophyton*, *Halisceptrum* and other Alcyonaria.

The facts presented by the bud-development of *Renilla* tend to show that a definite sequence in the appearance of symmetrically repeated parts may very readily be acquired or modified through the action of secondary causes which are, however, for the most part too obscure to be recognised.

§ 17. *Development of the zooids.*

a. The exhalent zooid.

The exhalent zooid (*ex.* in all the figures) makes its appearance some time after the appearance of the first pair of secondary polyps and always before the second pair are developed. It occupies always the same position, viz.: on the median line of the dorsal compartment a short distance in front of the pair of buds (fig. 181). Its early development is in all respects identical with that of the sexual polyps, and when the septa are well established they are found to have the same arrangement as in the latter. The ventral chamber is very narrow and remains always without a calyx-tooth. As the zooid increases in size a short calyx-tooth appears on each of the other chambers, and these are developed simultaneously so far as observed (figs. 188, 189). The zooid is in this stage closely similar to the mouth of the cell of a sexual polyp when the latter is contracted (*cf.* fig. 189). The zooid remains in essentially the same condition during its whole existence, but the calyx-teeth become much more elongated and the ventral chamber becomes so small as almost to disappear. No tentacles are ever developed and I have never observed the least rudiment of them.

We find that the dorso-ventral axis of the zooid, which may at once be determined by the elongation of the mouth and the position of the ventral compartment, coincides with the long axis of the primary polyp; and furthermore that the ventral side is turned towards the posterior part of the latter. This relation of the axis is constant, though the axis of the zooid sometimes forms a small angle with the long axis of axial polyp. It sometimes happens that two exhalent zooids are formed. In this case one of them is usually placed in the normal position and the other lies at one side with its axis more or less oblique. In one case the zooid was devoid of a mouth-opening.

b. The inhalent zooids.

An especial interest attaches to the development of these zooids on account of the curious and constant relations existing between their axis and between these and the axis of the sexual polyps.

The zooid develops in quite the same manner as the young sexual polyp or the exhalent zooid, but never progresses beyond the stage in which two calyx-teeth (those of the ventro-lateral chambers) are formed. The zooid is therefore structurally as well as physiologically (see p. 784) identical with the young sexual polyp. In the fully-developed zooid the œsophagus is of an oval form, elongated slightly in the dorso-ventral axis, and connecting with the exterior through an oval mouth. The inner wall of the œsophagus is covered on its ventral side with powerful cilia, by the action of which water may be drawn in from the exterior in precisely the same manner as by the young sexual polyps. The mouth is furnished with a sphincter muscle by which it may be tightly closed when the cavities of the colony are sufficiently distended with water. As already described, the sexual buds, as they increase in size, gradually cease to perform the function of drawing in water. The zooids, however, retain this function permanently and have been specialised for this purpose alone since they have neither tentacles, mesenterial filaments, nor reproductive organs. The sexual buds hand over their early function, as it were, to the zooids as they become themselves adapted to play another part in the economy of the organism.

As shown in fig. 202 the two calyx-teeth of the zooids become greatly elongated and in some specimens, especially in the posterior parts of the disc, may attain an enormous development. Their walls are soft and flexible and are considerably thickened towards the tips where the cells assume a columnar form. It seems very probable that they may perform tactile functions, but I have been unable to demonstrate this in living specimens.

The chambers have the usual arrangement, there being always a somewhat narrow ventral chamber enclosed between two wide ventro-lateral ones. The five upper chambers are always smaller than the ventro-lateral ones and are nearly equal in size. It is therefore always easy to distinguish the dorso-ventral axis of the zooid, which for the sake of brevity I shall call simply the *axis*.

The zooids are produced in pairs like the sexual polyps, though with less regularity. The first pair (fig. 185, z^1.) make their appearance on the dorsal side of the axial polyp near the bases of the first pair of sexual polyps, at the time when four or five pairs of sexual polyps have appeared. Behind these there appear two or three pairs of zooids somewhat irregularly placed on the upper side of the axial polyp. They are arranged (*cf.* figs. 188, 189) on either side of a longitudinal space which remains permanently free from zooids and is very conspicuous in the fully-formed colony. KÖLLIKER has termed this area the *keel* (Kiel), and it is of common occurrence among the Pennatulida. In the adult colony it extends forwards from the posterior sinus about half-way across the disc. The exhalent zooid is placed at its anterior end and groups of inhalent zooids border it on either side. The axes of these zooids are very irregularly placed, but as a rule the ventral side of the zooid is turned towards the posterior part of the colony.

The remaining zooids appear on the dorsal side and in the median line of the sexual

polyp-cells, and a constant relation exists between the axis of the zooids and of the polyps on which they are placed. For the sake of convenience I shall term these zooids *dorsal zooids* to distinguish them from the *marginal zooids* which border the keel.

Four dorsal zooids, to begin with, make their appearance on the upper side of each polyp-cell. They are formed successively, proceeding from the base of the polyp outwards towards the oral extremity, as may be seen upon comparison of figs. 187, 188, 189. In fig. 187 the polyp p^5. has a single dorsal zooid, and p^3. has two. In fig. 189 the polyp p^3. has three zooids and p^7. has four.

The bilateral arrangement of the zooids is well shown by fig. 187, in which the positions of the zooids are accurately represented. With two exceptions each zooid has its counterpart on the opposite half of the colony. The exceptions are the marginal zooid *zm.*, and the dorsal zooid *zd.*, which appear on the right side only.

The zooids are sometimes formed on very young sexual buds, as at p^4. in fig. 187. This recalls the very early appearance of the power of budding in the axial polyp. Upon examining the axis of a dorsal zooid we find that in many cases it coincides with the long axis of the sexual polyp on which it is seated, and where it does not the axis of the zooid forms less than a right angle with that of the polyp. Moreover, the ventral chamber of the zooid is always placed at that end of the axis which is turned towards the basal part of the polyp and therefore towards the centre of the colony. There is a strong tendency in the zooid to assume a position on the secondary polyp corresponding with the position of the exhalent zooid with respect to the primary polyp (see p. 791); and the variations from this position caused by the greater or less obliquity of the axis must be considered as departures from the type. Upon the axial polyp only one zooid as a rule, though sometimes two, appears in front of the exhalent zooid.

Multiplication of the zooids.

The zooids have thus far been described as if remaining simple, as is really the case up to the stage shown in fig. 188. Soon after this, however, the zooids themselves become centres of multiplication and each zooid becomes the parent of a whole group of secondary zooids. It is therefore necessary to distinguish primary and secondary zooids as we have recognised primary and secondary sexual polyps.

The axis of the primary dorsal zooid, as we have seen, stands in a definite relation to that of the sexual polyp. The axes of the secondary zooid, on the contrary, show no direct relation to those of the sexual polyp *but to those of the primary zooid.* Hence we must regard the latter as the real parent of the secondary zooids, though these appear to arise as buds on the dorsal side of the polyp-cell and not directly upon the primary zooid. We must, at any rate, grant that the primary zooid is a centre of force which controls the development of the secondary zooids, and it will be convenient for our purpose to consider the latter as the progeny of the former.

The multiplication of the zooids varies exceedingly, as we might expect from their

rudimentary structure and great numbers, but the variation affects only the number and arrangement of the zooids, leaving the relations between their axes unaltered. Figs. 194 to 203 illustrate the multiplication from a simple zooid (fig. 194) to a group of eighteen. The figures, it will be understood, are not drawn from different stages of an individual group but represent a number of different groups in various stages of development.

In what may be regarded as the typical case a group of four zooids is first formed (fig. 199). The upper one (*d.*), situated at the dorsal side of the primary zooid (*p.*), is usually first to appear (figs. 195–197,) but the lateral zooids (*l.l.*) may appear, singly or together, before the upper one (see fig. 198). In the group of four the primary zooid is distinguished by its greater size and by the possession of calyx-teeth on the ventro-lateral chambers. The ventral chambers of the zooids (*v.*) are turned away from the centre of the group. Thus the axes of the lateral zooids form an angle of 90° with that of the primary zooid, and the axis of the upper zooid is 180° from that of the primary zooid.

New zooids now make their appearance in irregular succession in the angle between the four already formed (figs. 200–202) so that the group then consists typically of eight zooids. The same relation of the axes holds good for the new zooids —*i.e.*, the ventral chamber is turned outwards, or away from the centre of the group. The superiority in size of the primary zooid is still marked and its calyx-teeth are very well developed. In most, though not in all, cases the upper zooid also acquires a pair of calyx-teeth as shown in the figures, and sometimes one of the lateral zooids also (fig. 202, *l.*). Most of the secondary zooids remain however without calyx-teeth, though the ventro-lateral chambers are always larger than the others. The ventral chamber is always very narrow in the zooids which have calyx-teeth, but in the other zooids it is often scarcely narrower than the ventro-lateral chambers. The axis of the zooid can however be always recognised by the elongation of the mouth and the crowding of the six upper septa.

Many of the subsequently formed zooids develop in the same manner as those already described, appearing in the angles between pre-existing zooids and having their ventral chambers turned away from the centre of the entire group. In some cases, however, the secondary zooids become in their turn centres of multiplication, thus forming minor groups which repeat, more or less completely, the formation of the primary group. This is shown in fig. 203. The primary zooid of the system is marked *p.*, and above it lies the dorsal secondary zooid (*d.*) corresponding with the upper zooid in fig. 199. A considerable number of the lateral zooids are simple and their axes are related to that of the primary zooid (as may be seen from the position of their ventral chambers *v.v.*). At *x.*, however, is a group of four zooids which are arranged about a centre of their own and form a secondary group quite similar to the primary group shown in fig. 199. The principal zooid (p^{11}.) of this secondary group has the usual position with respect to the primary group and appears to correspond with

the zooid x. of fig. 202. The three other zooids are evidently placed with reference to p^{II}. and not to p^{I}. Thus the zooid d''. has its ventral chamber turned *towards* the centre of the main group and *away from* that of the secondary group. Hence d''. is the offspring of p^{II}. and the grandchild of p^{I}.

There appear to be in fig. 203 two other secondary centres, but each is represented by two or three zooids only. Thus a, b, and c seem to be arranged about the centre y, while d', e, and perhaps f, are arranged about a centre at z. It is rare to find the secondary groups completely or symmetrically formed, and in many, perhaps most, cases no secondary centres can be certainly identified. In fact, I have seen only two cases in which the secondary groups were as perfectly formed as at x. in fig. 203.

Review.

The close correspondence between the mode of budding of the zooids and of the sexual polyps must already have struck the attention of the reader. If the group of four zooids shown in fig. 199 be compared with the group consisting of three sexual polyps and the exhalent zooid (fig. 181) the composition of the two groups is found to be the same. If the axial polyp in fig. 181 be turned upwards at its anterior part, as actually happens at a later stage, it will have the same relation to the exhalent zooid as that existing between the lower and upper zooids of fig. 199, and the two lateral buds in fig. 181 when turned upwards have precisely the same position as the lateral zooids in fig. 199.

Similarly, we may compare the group of eight zooids (fig. 202) with the groups of eight shown in figs. 184, 205 and 206 (these are seen from the ventral side so that the dorsal member of the group, the exhalent zooid, does not show directly). It is scarcely necessary to remind the reader that I do not mean that the corresponding members of the two groups are homologous with each other, but only that they have been produced by a similar form of asexual multiplication.

Summing up these results, we find that the multiplication of the zooids conforms to a definite law, which upon comparison is found to be identical with that which rules the budding of the sexual polyps.

§ 18. *Closure of the peduncular canals.*

We have finally to describe the manner in which the two canals of the peduncle become closed in front and thus complete the canal-system. As described in the introduction, these canals are in the adult completely closed in front, whereas in the young they communicate freely with the gastric cavity of the axial polyp.

a. The dorsal canal.

The closure of the dorsal canal is effected by the free edge of the peduncular septum growing forwards and finally uniting with the dorsal wall just anterior to the exhalent

zooid. This is illustrated by figs. 204 to 207. In fig. 204 the free edge (*e.*) is still some distance behind the zooid (*ex.*). In the next figure it has advanced further forwards and in fig. 207 has nearly passed the zooid. The edge finally unites with the dorsal wall at about the stage of fig. 187 and the canal is completely closed. These stages in the forward movement of the edge of the septum are shown also in dorsal view in figs. 181, 186 and 185.

As the septum travels forwards its edge stretches between the bases of the dorsal pair of septa and the latter gradually extend down upon the lower side of the peduncular septum in a manner which it is difficult to describe, and is scarely shown in the figures. In fig. 181 the edge may be seen stretching between the dorsal septa far behind the dorsal mesenterial filaments (*d.f.*). In fig. 205 the edge of the septum and the filaments have nearly met. In fig. 206 the lower ends of the dorsal filaments lie below the peduncular septum, and in fig. 207, finally, the filaments and septa lie for more than half their length on the lower side of the peduncular septum.

b. The ventral canal.

The closure of this canal is effected by an entirely different process which I have not been able to follow out completely. It has already been mentioned (p. 786) that the partition between the first two sexual buds on each side ends below by a free edge (fig. 204). From this point a delicate flap or fold of membrane extends for a short distance inwards on the under side of the peduncular septum (fig. 204, *fl.*). The latter bends rather suddenly upwards at this level to terminate by the free edge (*e*). in front. In a later stage these flaps extend still further inwards so as nearly to meet on the under side of the septum. The edge of the flap also extends obliquely upwards and forwards across the base of the bud (fig. 205). Still later the two flaps unite below the peduncular septum and form a single membrane extending entirely across the upper part of the ventral canal and ending by a smooth round edge below (fig. 206). At the sides the membrane is slung to the body-wall by fibrous strands like those which suspend the peduncular septum (see p. 768), and it now extends nearly across the base of the bud.

In the latest stage observed (fig. 207) the membrane extends at the sides nearly around the body and has united with delicate irregular outgrowths from the ventral and ventro-lateral septa. Thus the ventral canal is separated by an incomplete partition from the anterior part of the axial polyp where the septa, mesenterial filaments and other organs are situated. There is still, however, a very large rounded opening in the middle of the partition through which the currents of the gastric fluid still flow. In later stages this opening closes up completely, probably by the approximation and union of the edges of the membrane, but I have been unable to follow this since the walls of the body become very opaque through the appearance of great numbers of spicules.

In the adult the peduncular septum appears to be split horizontally in front into two

layers between which lies the cavity of the axial polyp. The development of the parts shows that this is not really the case. The upper layer alone is a direct continuation of the septum, while the lower layer is a secondary formation produced by outgrowths from the walls of the body and the septa.

The specimen represented in fig. 207 shows an interesting abnormal condition of the tentacles which deserves mention. When first discovered the two lower lateral tentacles on the left side of the axial polyp were aborted, possessing only a single pair of rudimentary pinnæ. *The two corresponding tentacles of the first lateral bud on the same side were aborted in a precisely similar manner* (see the figure). The specimen was kept alive for a fortnight, but unfortunately died before the other buds had acquired their tentacles. Meanwhile the aborted tentacles grew to about half the size of the normal ones.

The rudimentary condition of the two corresponding tentacles in the primary and secondary polyps may have been due to accidental mutilation, but the chances against such a coincidence seem very great. If on the other hand it were due to the inheritance by the bud of a mutilation or monstrosity in the parent the case would be very interesting.

IV.

GENERAL CONSIDERATIONS.

§ 19. *The systematic relations of* Renilla.

In reviewing the development of the *Renilla* colony, we are naturally led to inquire whether the arrangement and succession of the buds throws any light on the relations of *Renilla* to other members of the Pennatulacea. Here, as in the case of the homologies of the organs of the individual, the basis for comparison is very narrow on account of the imperfect state of our knowledge. Fortunately, however, the evidence is enough to show how the mode of budding in *Renilla* may readily be reduced to the ordinary type as exhibited in the penniform Pennatulids, as for instance in *Pennatula* or *Pteroides*.

Kölliker was so fortunate as to obtain a very young colony of *Pteroides Lacazii* (Köll.), a representative of the typical Penniformes, and his valuable and interesting observations, when compared with my own on *Renilla*, are enough to show that the mode of growth is essentially the same in these widely different forms. In *Pteroides* ('Pennatuliden,' p. 356, plate xxiii., figs. 214, 215) as in *Renilla* there is a primary or axial polyp which produces paired lateral buds; the order of their appearance was not determined nor was it ascertained whether new buds are interpolated between older

ones. The young colonies of *Renilla* and *Pteroides* are in this stage essentially alike, as may be seen on comparison of KÖLLIKER's fig. 214 (*Pteroides*) with my figs. 186 or 187. In both, the axial polyp terminates in the median line in front and the structure of the colony is strictly bilateral.

The subsequent history of the axial polyp was not followed nor has this ever actually been done save in *Umbellularia*,* which is an exceedingly aberrant form, and may for the present be left out of consideration. Inferring its history, however, from a study of the adult forms, KÖLLIKER makes the following general statement (*l.c.*, p. 420): "Die typische Bau dieser Stöcke ist ohne Kenntniss ihrer Entwicklung nicht zu verstehen, und bemerke ich daher vor Allem, das der erste aus dem Embryo hervorgehende Polyp, den ich den Haupt, oder axial Polypen nenne, wahrscheinlich nicht überall in derselben Weise sich verhält. Bei den Einen Formen, wie bei den *Veretilliden, scheint derselbe sich zu erhalten* und später, wie die secundär aus ihm entstandenen Individuen, einfach als Geschlectsthier zu wirken. Bei andern Abtheilungen dagegen, wie bei den *Pennatuleen*, und *Renillaceen, verkümmert der axial Polyp schon früh* und stellt gewissermassen *ein rein* vegetatives Individuum dar, dessen Function erlischt, sobald eine gewisse Zahl secondäre Einzelthiere gebildet sind. Sei dem wie ihm wolle, so bilden sich auf jeden Fall die späteren Einzelthiere *als seitliche Knospen* au dem ersten Polypen und beruht auf einer fortgesetzten solchen Knospenbildung wesentlich die Entstehung der ganzen Colonie."

This statement must be slightly modified, so far as the Renillaceæ are concerned; for the axial polyp does not in this case abort but remains, as in the *Veretillidæ*, as a sexual-feeding polyp (KÖLLIKER's statement is evidently made under the assumption that the exhalent zooid—"*Hauptzooid*"—is the aborted axial polyp, a view which has been shown to be erroneous).

Furthermore it is not certain that the axial polyp, even in the elongated *Penniformes* and *Virgularieæ*, remains at the anterior end, increasing in length throughout the growth of the colony; for WILLIMÖES-SUHM observed (*l.c.*) that in *Umbellularia* the axial polyp does not retain its original position in the median plane, but becomes bent to one side so as to assume a lateral position, its former place being taken by one of the secondary lateral buds. Still, the evidence seems to be upon the whole in favour of the view that the primary polyp, whether remaining functionally active or becoming aborted, does retain its median position in the elongated Pennatulids and forms the central axis of the community.

In the simple elongated Pennatulids—as in the *Bathyptileæ* of KÖLLIKER—the axial polyp produces a series of simple lateral buds on each side, which have a bilaterally symmetrical arrangement, and remain simple throughout the life of the organism. From this condition, as KÖLLIKER fully shows, a nearly complete series may be formed on the one hand through the *Protoptileæ*, *Funiculineæ*, *Virgularinæ* to the typical *Penniformes*, and on the other hand through the *Kophobelemnonieæ* to the *Veretillidæ*.

* WILLEMÖES-SUHM, Ann. and Mag. of Nat. Hist., vol. xv., 1875

Upon comparison we find that the colonies of *Pteroides* and *Renilla*, though widely different in their adult state from each other and from the *Bathyptileæ*, pass through a stage of development which precisely corresponds with the permanent condition of the latter group. Obviously this fact tells strongly in favour of the derivation of both the *Penniformes* and the *Renillaceæ* from the *Bathyptileæ* or a representative group, and this is the conclusion which upon the whole appears to me most probable. So far as the *Penniformes* are concerned this conclusion is simply a reiteration of Köllıker's conclusions, but in regard to the *Renillaceæ* it is entirely different. Köllıker's view is as follows ('Pennatuliden,' p. 450):—

"Nur zu den *Renilliden* führt keine Brücke von den jetzt lebenden Pennatuliden aus und müssen wir zum Verständnisse derselben auf eine noch nicht beobachtete Urform, ähnlich den jugendlich von Fritz Müller beobachteten *Renillen* oder den Cornularien unter den Alcyoniden, zurückgehen, die der Kürze halber *Archiptilum* heissen mag. Dieses *Archiptilum* wäre also als ein freier einfacher Polyp nach Art der Edwardsien aber mit der innern Organisation der Alcyonarien zu denken und liesse ich an ihm schon eine solche Differenzirung annehmen, dass ein Stiel und ein Kiel zu unterscheiden wäre. Aus solchen Archiptileen oder weiteren Umbildungen derselben könnte man dann einerseits durch besondere Art der Knospenbildung die *Renilliden*, anderseits die Protoptileen und die Bathyptileen ableiten und wäre im ihnen das vereinigende Band der ganzen Ordnung gegeben. Die Abkunft der Archiptileen selbst anlangend, so werden wir naturgemäss auf die Hydroidpolypen geführt und kann es nach dem, was wir über den Bau von *Hybocodon*, *Tubularia*, und *Cormorpha* wissen, keine Schwierigkeiten machen, von denselben aus den Uebergang zu den gekammerten Anthozoen zu finden wie dies auch Haeckel angedeutet hat. Diese Protanthozoen würden dann in weiterer Linie zu den Urtypen der verschiedenen Abtheilungen der Korallthiere und somit auch zu den Archiptileen sich entwickelt haben."

The development of the *Renilla* colony shows, however, that it is unnecessary to go back further than the *Bathyptileæ*, so far at least as the mode of budding is concerned. The peculiar form of the colony is a result primarily of the circumstance that *the longitudinal growth of the axial polyp ceases at an early stage*, while the two series of lateral buds continue to extend forwards until they enclose the axial polyp; and secondarily of the fact that new lateral buds are constantly interpolated between those already formed, and that the lateral buds fuse with each other to some extent. If we imagine the axial polyp in fig. 189 to become greatly elongated, so as to separate the older buds from one another, and thus to leave room for the younger buds between them, we should have a colony similar to the *Bathyptilum*, *i.e.*, a long central axis with a single series of lateral buds on each side.

Köllıker's view of the derivation of *Renilla* involves one serious difficulty on any monophyletic theory of descent. The original simple progenitor of the Alcyonaria cannot have possessed the *septum transversale* or the four peduncular septa of the higher Pennatulids, since these are structures peculiar to the Pennatulacea, and do

not exist so far as known in the simple young of other Alcyonaria (*cf. Leptogorgia*, p. 768). It is hard to avoid the conclusion that these structures are intimately connected with the formation of the peculiar internal axis in those Pennatulids (including all but *Renilla*) which possess such a structure. In *Renilla reniformis* the *septum transversale* alone is developed (as the peduncular septum), but in *Renilla amethystina*, as described by Kölliker and Eisen, four partitions appear in the anterior part of the peduncle (see p. 770), which appear to be homologous with the four peduncular septa by which the axis is suspended in the axis-bearing Pennatulids. If, then, the latter forms and *Renilla* have independently arisen from the *Archiptilum*, which possesses no axis, it is impossible to account for the presence of the four peduncular septa in some species of *Renilla*. Whereas, if *Renilla* is descended from an axis-bearing form resembling *Bathyptilum* the occasional appearance of four peduncular septa presents no difficulty (compare § 9).

As Kölliker has shown, the lateral pinnæ (*Blätter*) of the *Penniformes* are probably derived from simple lateral buds by the appearance of a series of dorsal buds upon the latter:—

"In der That lehren die Pennatuliden mit Blättern, dass jedes Blatt anfänglich nur aus wenigen, wahrscheinlich ursprünglich nur aus Einem Polyp besteht und dass die übrigen Individuen nach und nach an der *Dorsalseite* desselben *aus ihm hervorbilden*, was theils durch *Theilungen*, theils durch *Knospenbildungen* aus ihm geschieht" ('Pennatuliden,' p. 430).

At first thought it might seem probable that this dorsal series of buds is represented in *Renilla* by the series of dorsal zooids which always appear on the upper median line of the sexual polyps. But upon examination we find that the axes of the zooids are differently placed from those of the polyps. The ventral chambers of the former face inwards (towards the centre of the disc), whereas those of the polyps in the pinnæ of the *Penniformes* face backwards; it seems therefore improbable that they can correspond. As we shall see in a following section, it is doubtful whether the zooids of *Renilla* are homologous with (*i.e.*, directly descended from) sexual polyps. The representatives of the dorsal polyps of the pinnæ, if present at all in *Renilla*, are rather to be sought in those lateral buds of *Renilla* which do not arise directly upon the body of the axial polyp.

Summary.

The development of the colony in *Renilla* indicates its ancestral origin from a form resembling the *Bathyptileæ* from which have also been derived along different lines of descent the *Pennatuleæ* on the one hand, and the *Kophobelemnonieæ* and *Veretillidæ* on the other. In the course of this transformation an axis has probably been lost, the only indication of it at present being the persistence of the *septum transversale* (peduncular septum) and in some species of the four peduncular septa. No decisive

evidence on the latter question can be adduced until the development of the axis is made known.

§ 20. *Bilateral symmetry of* Renilla.

The very striking bilateral symmetry, both of the individual polyps and of the entire community, is constantly brought before our notice in studying the anatomy and development of *Renilla;* and it is impossible to leave the subject without considering briefly the significance and origin of this symmetrical arrangement of parts.

Reviewing the symmetry of the individual, we find that is expressed, firstly, in the existence of a dorso-ventral axis, represented by certain median unpaired parts, viz.: the elongated œsophagus and mouth, the ventral chamber devoid of a calyx-tooth, the dorsal chamber with a well-developed calyx-tooth, and the dorsal and ventral median areas of longitudinal muscles. All the remaining parts are bilaterally arranged with respect to this axis, viz.: the tentacles, calyx-teeth, septa, mesenterial filaments, reproductive organs, and the septal areas of longitudinal muscles. The tentacles have a nearly perfect radiate arrangement, but the arrangement of the other organs is, to say the least, as much bilateral as radiate. The bilaterality of the calyx-teeth is strongly expressed in their mode of development, since, with the exception of the dorsal tooth, they appear in successive pairs. The septa are arranged in pairs of different lengths, and are joined together at their lower ends in a strictly bilateral arrangement. The bilaterality of the mesenterial filaments is nearly as marked as that of the septa on account of their arrangement in pairs of different length, their structure and rate of development. The reproductive organs have a strictly paired arrangement, appearing only on the dorso-lateral and ventro-lateral septa. The longitudinal muscles of the septa finally show a marked bilateral symmetry in their arrangement, being always placed on the ventral sides of the septa.

The bilaterality of many of these parts must be of comparatively recent acquisition; for in other and lower polyps it is less evident or entirely wanting. Traces of bilateral symmetry are found in nearly all polyps, but in most of the lower forms (Zoantharia) radial symmetry, more or less complete, predominates. In the higher forms the radiating parts assume a more definitely bilateral arrangement which is very marked in the Alcyonaria and reaches its culmination in *Renilla.** Hence there can be no doubt that the bilateral structure is, in part at least, due to a rearrangement of parts which were formerly radially symmetrical. The bilateral symmetry is, as it were, built upon a basis of radial symmetry; and traces of the latter, more or less pronounced, may accordingly be seen in the bilateral arrangement of most of the parts of *Renilla.* Thus it exists almost unmodified in the grouping of the tentacles, in the septa has partly given place to a bilateral arrangement, and in the reproductive organs is scarcely or not at all to be recognised.

* See especially Haacke, "Blastologie der Korallen," Jena. Zeitschr., Bd. xiii., 1879, and Haeckel, "Generelle Morphologie" und "Studien z. Gastræa-theorie," Jena. Zeitschr., Bd. viii., ix., 1874–5.

In the community produced by the asexual multiplication of the individual, the bilateral symmetry is very nearly perfect. Such departures from perfect symmetry as do exist are inconstant, and appear to be due simply to slight inequalities of growth produced by varying conditions of nutrition. In the adult colony a middle plane is clearly marked by the form of the disc, position and internal structure of the axial polyp, position of the exhalent zooid and of the "keel," and the insertion of the peduncle. On either side of this axis the polyps and zooids are disposed with great regularity. Each sexual polyp has its exact counterpart on the opposite side of the disc, the axis of the two polyps making the same angle with the long axis of the colony. The groups of zooids also correspond pretty closely on the two sides, though less perfectly than the polyps.

The budding of the colony is at first strictly bilateral with surprisingly small variation; and this is true both of the polyps and of the zooids. In later stages the polyps assume a radiating arrangement, as may be seen in figs. 187 and 189, and a radial symmetry is therefore feebly indicated in the disc. This is however due simply to the cessation of growth in the long axis—*i.e.*, the axial polyp—and stands in no relation whatever to the radial symmetry of the individual. In this case we have a slightly marked secondary radial symmetry superimposed upon a primary bilateral form; and in this respect the symmetry of the colony exactly reverses the symmetry of the individual.

It seems clear therefore that the symmetry of the colony has been acquired independently of the symmetry of the individual, and it will be advantageous to consider separately the origin of the symmetry in the two cases.

If we examine the position of the individual polyps, we observe that they are so placed as to have a bilaterally symmetrical environment *which corresponds with the bilateral arrangement of their parts*. Below, they rest upon the sand; above, they are exposed to the water; so that the dorsal and ventral sides are very differently conditioned. The lateral conditions are, however, identical, since each polyp is closely united with a similar polyp on each side. It is impossible to avoid the conclusion that the bilateral environment stands in causal connexion with the bilateral structure, and the probabilities seem strongly in favour of the view that the bilateral structure —or, at least, some of its features—is a result of the environment. This view is in harmony with the prevailing general theories of symmetry which have been especially and independently developed by HAECKEL and SPENCER; namely, in SPENCER'S language, that the form of symmetry depends ultimately on the nature and distribution of the incident forces acting upon the organism. These theories are so familiar as to need no review here, and I will only refer to HAECKEL'S views concerning the ancestry of the Cœlenterata as developed in the papers upon the "Gastræa theory" to which reference has been made.

According to HAECKEL'S theory the Cœlenterate series has been evolved from a primitive ancestral "*Protascus*," immediately derived from the *Gastræa* by the

attachment of the latter at the base and the gradual acquisition of a radiate structure as a result of the equality in all directions of the lateral conditions. This theory leaves unexplained the bilateral symmetry which appears in a greater or less degree in all polyps, and HAACKE ("Blastologie der Korallen," *l.c.*) has endeavoured to explain this as the result solely of the formation of colonies. This author holds that in solitary forms like the Actiniæ the bilateral symmetry is due to descent from colony-building species, and he believes that the paired development of the septa is thus to be explained, though in precisely what manner he is unable to say.

Without accepting in all details HAACKE'S views, which are only a special application of the environment theory of HAECKEL and SPENCER, it appears to me highly probable that the nature of the environment of the individual polyps in the colony will satisfactorily explain their bilateral structure. It is, of course, impossible to explain exactly how the bilaterality of the various organs is related to the bilaterality of the environment on account of our imperfect knowledge of the functions of these organs and of the laws of growth. But we cannot admit that the perfect correspondence between structure and environment is due to mere accident, and the only alternative is to regard it as the result of adaptation in the organism.

An obvious objection to this view is that it may be putting the cart before the horse; for there may be laws of nutrition or of growth, dependent upon a bilateral structure already existing, which limit the production of buds to the sides of the axial polyp. But we have seen that the zooids—which are undeveloped buds—are produced in the dorsal sides of the polyps in *Renilla*, and KÖLLIKER has shown that in other Pennatulids the zooids may appear anywhere upon the polyps. All parts of the sexual polyps therefore possess equally the power of producing buds, and hence the circumstance that each polyp is laterally united with two other individuals depends on the general form of the colony and not upon any limitation existing in the laws of growth in the individual.

Passing now to a consideration of the symmetry of the colony, we find here the same general conditions as in the individual. The young colony, as we have seen, (p. 785) assumes a definite position as soon as it begins its sedentary life, and this position is maintained during the entire existence of the organism. In this habitual position of the colony, with the peduncle rooted in the sand and the disc expanded upon the surface, the dorsal and ventral sides are quite differently conditioned, while the sides are similarly conditioned. The conditions of nutrition within the colony being equally distributed, the rate of growth must tend to be equal upon the two sides, and any modifying agency must, so far as we can see, tend to be equal upon both. There seems to be no reason to doubt that such an equality of lateral conditions, if maintained for a long period of time, would ultimately produce as perfect a bilaterality as that of *Renilla*. It is unfortunate that so little is known of the habits of other Pennatulids in which the bilateral symmetry is less marked than in *Renilla*. It is probable that a study of these forms with reference to the relation between them

and their environments would throw further light upon the influence exercised by the environment upon the mode of budding and thus upon the symmetry of the colony.

§ 21. *Polymorphism of* Renilla.

Polymorphism has been definitely recognised as existing in the Pennatulacea since the publication of KÖLLIKER's great work so often cited in the foregoing pages, but the existence of "rudimentary individuals" was observed in *Renilla* by VERRILL many years earlier.*

We may distinguish in *Renilla* at least four kinds of individuals, viz.: *a*, the axial polyp; *b*, the secondary sexual polyps; *c*, the exhalent zooid; and *d*, the inhalent zooids. Possibly two classes of the latter should be recognised, viz.: zooids which possess a pair of calyx-teeth and those which are devoid of these structures.

The question now arises whether these various forms of individuals are to be regarded as morphologically equivalent—that is, whether all are to be considered as the direct descendants of originally similar individuals which have become modified in various directions for the physiological division of labour. There can be no doubt concerning the nature of the secondary sexual polyps, for these are identical in all essentials with the axial polyp. With the various forms of zooids, however, the case is different; for we have here to consider whether these are the aborted and rudimentary descendants of sexual polyps or are new formations which have never had a more highly organised structure than at present. To put the question in a concrete form we may inquire: Did the zooids during their past history ever possess tentacles, mesenterial filaments, and reproductive organs which were gradually lost as the polyps became specialised for the performance of a single function only, or had the zooids, when first developed in the colony, the same imperfect polypoid structure as at present?

The problem is the same as that presented by the Siphonophora, and in the latter case has given rise to the two totally different views with which everyone is familiar. On the one hand LEUCKART, VOGT, HAECKEL, CLAUS, and others regard the various parts of the Siphonophora (*Nectocalyces*, *Polypites*, *Hydrophyllia*, &c.) as the variously modified direct descendants of individuals which were once fully developed, though organically connected together. On the other hand we have the view especially urged by HUXLEY and METSCHNIKOFF, that these parts are only organs which never existed as fully formed individuals.

At first thought it would appear tolerably clear that the zooids of *Renilla* must have acquired their present structure simply through having degenerated from individuals resembling the sexual polyps. They agree closely with the latter in general structure, the differences consisting for the most part in the absence of organs

* "Revision of the Polyps of the Eastern Coast of the United States," Bull. Mus. Comp. Zool., Cambridge: 1864.

like the tentacles or mesenterial filaments, which could be of no use as the polyp gradually became exclusively adapted to the performance of a single function (taking in or discharging water). There are some structural details in the rudimentary zooid which seem scarcely explicable if not due to direct inheritance from a fully developed polyp. Such characters are the absence of a calyx-tooth from the ventral chamber and the presence of two long calyx-teeth on the ventro-lateral chambers. In some of the Pennatulids, according to KÖLLIKER, the zooids even possess a pair of mesenterial filaments on the two dorsal septa, and the presence of such rudimentary organs in the zooids would seem to be a strong indication of their descent by degeneration from sexual polyps.

A moment's consideration shows however an insurmountable difficulty in the way of this view. The zooids are far too numerous to have ever been represented by full-sized polyps, for there would not have been room for them on the colony. The dorsal zooids on a single polyp number from 20 to 70 or more in different species of *Renilla*, and it is obvious that even a far smaller number of full-sized polyps could not possibly have stood upon the dorsal side of a single individual. The same difficulty exists in many other Pennatulids, as in *Veretillum* or in some species of *Pennatula* (*e.g.*, *P. rubra*), where almost the entire ventral surface is covered with closely set zooids.

Hence the sexual polyps and the zooids cannot be regarded as equivalent members of the community, for they are not divergent modifications of identical ancestral forms. The zooids are new formations, acquired after the rest of the colony was established. In this case the question as to the "individuality" of the zooid is merely a verbal one; for if descent be made the criterion we cannot consider them such, and yet they are absolutely indistinguishable from young polyps. The interesting point is that buds may appear in a colony which never attain full development as ordinary individuals but are arrested at an early stage, before they have acquired all of their organs, and made to play a part in the physiological division of labour. If polymorphism thus produced may occur in the Pennatulid community, there is no reason why it may not occur in the Siphonophora, and it is possible that some of the members of the latter organism may have had such an origin. These members may be called "individuals" or "organs which simulate individuals," according to our fancy, the distinction being merely verbal.

Such a view would perhaps partially reconcile the conflicting views respecting the nature of Siphonophora referred to at p. 804. It is admitted by the advocates of the polymorphism theory that some of the structures of the Siphonophora—as, for instance, the tentacles—are not to be regarded as modified individuals ("Persons" of HAECKEL) but are simply organs belonging to the true individuals, though they cannot be distinguished from the latter by their ontogenetic development. It is not improbable that other members of the organism—for instance, the hydrophyllia or pneumatocysts—may have the significance of imperfectly developed buds which owe their origin not to degeneration from more highly organised individuals but to arrest of development

at an early age. The possibility still remains that some other members—for instance, the feeding polyps or the nectocalyces — may be the direct descendants of fully-developed functional individuals which have become adapted to different functions in the physiological division of labour.

The possibility must be borne in mind that the various members of a compound organism are not necessarily of morphological equivalence — which is simply a convenient term to denote identity of ancestral origin—and that, according as the members are or are not equivalent, different forms of polymorphism are to be distinguished. In some cases, as among some Hydroida, the polymorphism seems clearly the result of a physiological division of labour among members which were originally completely and similarly developed as individuals. Such communities alone can be regarded as polymorphic in the sense in which this term was originally applied by Leuckart to the Siphonophora. The polymorphism of *Renilla* and other Pennatulid colonies has probably had in part a different origin and such cases must be clearly distinguished from typical polymorphism. For example, in some Pennatulids two distinct forms of secondary polyps may be recognised, viz.: feeding polyps possessing tentacles and sexual polyps destitute of tentacles. These two forms are probably to be regarded as differently modified descendants of sexual polyps like those of *Renilla*, in which the functions of nutrition and reproduction were united. To this extent the colony is therefore polymorphic in the ordinary sense. The remaining members of the community, viz.: the zooids, have however, probably had a different origin, since they are buds which never attain to complete development and never did so in the past.

The zooid is in every respect—physiological as well as anatomical—identical with the young bud which is destined to form a sexual polyp. Moreover the zooid may in some Pennatulids under some circumstances actually develop into a polyp, as Kölliker states, and I have myself observed. The zooid is to be regarded therefore as a bud in a state of arrested development, which has however acquired the power of asexual multiplication.

We must therefore consider the difficult question as to the agency which originally caused the arrest of development in the buds. How, it may be asked, can in the first place a bud have been produced identical in all respects with the buds which are to form mature polyps, and yet incapable of full development?

It is perhaps impossible to give a complete answer to this question, but the key to the solution of the problem lies possibly in the fact that the zooid, although in an embryonic state, possesses nevertheless the power of asexual multiplication. As pointed out on a preceding page, the secondary zooids of a group are to be regarded as offspring of the primary zooid and not directly of the sexual polyp on which they are placed. We may therefore explain their rudimentary structure as the result of inheritance from the primary zooid, and hence have only to consider how the latter can have been produced.

It has already been stated that the primary zooid is almost always larger and more perfectly developed than the secondary zooids derived from it. If, then, the secondary zooid owes its rudimentary structure to inheritance from a slightly more advanced bud, may not the primary zooid, as Dr. W. K. Brooks has suggested to me, have been produced by the multiplication of a still more perfect bud, like the zooid, for instance, of *Halisceptrum* which possesses a pair of mesenterial filaments? This in turn may have been formed by the multiplication of a more highly organised bud, and so on until a fully developed polyp stood at the beginning of the series. This will be rendered more clear by an illustration, in the consideration of which it is necessary to bear clearly in mind the fact that the immature bud of the sexual polyp performs the same function as the zooid and that this function is of vital importance to the organism.

Suppose a secondary bud, A, to give rise by asexual multiplication to a tertiary bud, B, which remained longer in a rudimentary state and developed less perfectly than A, and hence performed more perfectly the function of taking in water. In a succeeding generation B gives rise to still more rudimentary individuals, C, and so on through many generations until true zooids, permanently rudimentary, were produced. The functions of the rudimentary and of the fully developed individuals being entirely different, the intermediate or transitional forms would perform both functions less perfectly. They would therefore tend to disappear by natural selection until a colony would result like *Renilla* in which no well-marked transitional forms existed. Such a process is widely different from direct degeneration since each stage of the series is not represented in the preceding stage. Thus in the foregoing illustration C is not represented in the preceding stage by B, but is an entirely new individual produced as a bud upon B; and this is true of each succeeding stage. If, then, the ancestral history of a zooid could be followed backward from one generation to another we should not find it becoming more and more highly organised, but a point would be reached when it would entirely disappear.

This view is perhaps of too speculative a nature to be accepted without reserve, but it has at least the merit of showing how structures like zooids, of considerable complexity, might suddenly arise without direct descent from or the gradual modification of any corresponding structures in a preceding generation.

In regard to the nature of such structures as the zooids, Huxley's definition of the "organs" of the Hydrozoa appears to me most satisfactory. They are, namely:—"Organs which tend more or less completely to become independent existences or zooids." (The term zooid is here used in a general sense and not in the special sense employed in this paper.) A careful distinction must, however, be drawn between these "organs" and those which are due to the direct degeneration or other modification of complete individuals; and the possibility must be borne in mind that these different kinds of structures may co-exist in the so-called polymorphic communities.

Beaufort, N.C., August 1, 1882.

[*Appendix.*—During the passage of this paper through the press, I have discovered in several genera of Alcyonaria that the dorsal filaments are, in fact, ectodermic downgrowths from the stomodæum, whereas the six others are strictly entodermic structures. My failure to recognise this fundamental difference was due to the circumstance that the entodermic filaments become at an early stage perfectly continuous with the stomodæal ectoderm, like the dorsal filaments, and my most favourable sections happened to be in every case through the entodermic filaments. For a description of these new observations I must refer to a forthcoming paper in the 'Mittheilungen aus der Zoologischen Station zu Neapel.'—Naples, September 20, 1883.]

Explanation of Figures.

The following lettering is used uniformly in all the figures. Other reference letters are explained for the separate figures. The figures of sections are with a few exceptions drawn with the camera. Those of the segmenting eggs and of the external appearances of the colony are free-hand.

al. Gastric cavity.
ax. Axial cells of peduncular septum.
c. Central cells.
c.m. Circular muscles.
ch. Radial chamber.
cx. Calyx-teeth.
d.c.x. Dorsal calyx-tooth.
d.l.ch. Dorso-lateral chamber.
d.l.f. Dorso-lateral mesenterial filaments.
d.l.s. Dorso-lateral septa.
d.s. Dorsal septa.
d.f. Dorsal mesenterial filaments.
e. Free edge of peduncular septum.
ec. Ectoderm.
en. Entoderm.
ex. Exhalent zooid.
f. Mesenterial filament.
l.m. Longitudinal muscles.
œ. Œsophagus.
p^1., p^2., p^3., &c. Sexual polyps, or buds destined to become such, numbered in the order of their appearance.
ped. Peduncle.

p.s. Peduncular septum.
s. Septa.
s.l. Supporting lamella.
sp. Spicule or spicule cell.
st. Stomodæum.
t. Tentacle.
v. Ventral chamber or ventral side.
v.s. Ventral septa.
v.cx. Ventral (ventro-lateral) calyx-teeth.
v.f. Ventral mesenterial filaments.
v.l.s. Ventro-lateral septa.
v.l.f. Ventro-lateral mesenterial filaments.
v.l.ch. Ventro-lateral chamber.
y. Yolk.
z. Inhalent zooids.

PLATE 52.

Figs. 1 to 14. Segmentation of an egg which divides at first into eight spheres. Time as follows:—Fig. 1, 8.50 A.M.; 2, one minute; 3, two m.; 4, seven m.; 5, ten m.; 6, twenty-five m.; 7, thirty-four m.; 8, fifty-five m.; 9, sixty-three m.; 10, sixty-eight m.; 11, seventy-five m.; 12, ninety m.; 13, ninety-eight m.; 14, one hundred and fifteen m. ×85.

Figs. 15 to 18. Continuation of segmentation, from another specimen. Time as follows:—Fig. 15, 10 A.M.; 16, ten m.; 17, twenty-seven m.; 18, thirty-two m. ×85.

Figs. 19 to 24. Unusual mode of segmentation. Time as follows:—Fig. 19, 7.55 A.M.; 20, two m.; 21, ten m.; 22, twenty m.; 23, twenty-three m.; 24, forty m. ×65.

Figs. 25 to 27. Division of an egg into two spheres. ×65.

Figs. 28, 29. Egg divided into four spheres. ×65.

PLATE 53.

Figs. 30 to 37. Segmentation of an egg which divided at once into sixteen spheres. Time not recorded. ×65.

Figs. 38 to 41. Unequal segmentation beginning with sixteen spheres. Time as follows:—Fig. 38, 9.7 A.M.; 39, same in different position; 40, thirty-three m.; 41, thirty-six m. ×65.

Figs. 42 to 44. Another specimen illustrating unequal segmentation beginning with

sixteen spheres. Time:—Fig. 42, 9.20 A.M.; 43, same in different position; 44, thirty m. ×65.

Figs. 45 to 48. Segmentation of an egg which first divided incompletely into eight spheres, and afterwards completely into sixteen. Time:—Fig. 45, 9.5 A.M.; 46, five m.; 47, twenty-one m.; 48, thirty-three m. ×65.

Figs. 49 to 58. Segmentation of an egg which first divided irregularly and incompletely into eight. The sphere marked *a* failed to divide with the others at the third cleavage but divided at the fourth (57). Time:—Fig. 49, 10.29 A.M.; 50, four m.; 51, six m.; 52, fifteen m.; 53, different position, seventeen m.; 54, thirty-one m.; 55, forty-one m.; 56, forty-eight m.; 57, fifty-six m.; 58, sixty-eight m. ×65.

Figs. 59 to 62. "Partial" or progressive form of segmentation. Time:—Fig. 59, 10.6 A.M.; 60, eight m.; 61, nineteen m.; 62, same in different position. ×65.

Figs. 63 to 67. Segmentation similar to the last. Time:—Fig. 63, 11.35 A.M.; 64, nine m.; 65, thirteen m.; 66, nineteen m.; 67, twenty-one m. ×65.

PLATE 54.

Figs. 68 to 72. Very unequal and irregular form of segmentation. Time:—Not recorded. ×65.

Figs. 73 to 76. Segmentation of *Leptogorgia*. Time:—Fig. 73, 10.14 A.M.; 74, three m.; 75, twenty-one m.; 76, thirty-six m. ×70.

Figs. 77 to 85. Further segmentation of *Leptogorgia*; another specimen. Time:—Fig. 77, 10.5 A.M.; 78, fifteen m.; 79, twenty-four m.; 80, thirty-five m.; 81, seventy-eight m.; 82, ninety-five m.; 83, one h. fifty-five m.; 84, two h. five m.; 85, two h. twenty-five m. ×70.

Fig. 86. Section through unfertilised egg showing germinal vesicle and spot, *d*. ×85.

Fig. 87. Section through egg immediately before segmentation. ×85.

Fig. 88. Section through the same egg, separated from the last section by three intervening ones. ×85.

Fig. 89. Section through an egg in the act of division into sixteen spheres, directly from the unfertilised egg. ×85.

Fig. 90. Section through an egg which from the exterior appeared to consist of eight spheres. ×85.

Fig. 91. Section through an egg with sixteen superficial spheres and a central unsegmented mass. ×85.

Fig. 92. Similar to the last but with the central mass much reduced. ×85.

Fig. 93. The spheres now extend to the centre of the egg and the central mass has nearly vanished. ×85.

Fig. 94. Blastula, with distinct segmentation cavity. One of the spheres, *a*, is apparently undergoing a delamination cleavage. ×85.

Fig. 95. Egg in resting stage with unsegmented central mass. ×190.

PLATE 55.

Fig. 96. In this embryo the inner ends of the spheres are separating or have just separated from the outer portion. ×190.

Fig. 97. Delamination completed. ×145.

Fig. 98. Unsegmented egg or one in the act of division. To show vertical amphiasters. ×85.

Fig. 99. Section through an egg in which the delamination is partially accomplished but is in progress in the cells *a* and *b*. The section is incomplete below but complete above. ×85.

Fig. 100. Later stage; the last to show delamination still in progress. The section is complete above and below but incomplete on the sides. ×85.

Figs. 100^a., 100^b., 100^c. Three larvæ of about twelve hours to show irregularity in form. ×65.

Fig. 101. Free-swimming larva of about twenty-four hours. ×45.

Fig. 102. A slightly older larva under compression, showing septa. The ventro-lateral septa could not be followed up to the peduncular septum as it ordinarily can. ×45.

Fig. 103. Larva of about three and a-half days' showing septa and buds. Dorsal view. ×45.

Fig. 104. The same larva, from left side. ×45.

Fig. 105. Same specimen shown in figs. 103 and 104 in a state of strong contraction. ×45.

Fig. 106. *Leptogorgia*. Same embryo shown in figs. 77 to 85, ten minutes later than fig. 85. ×70.

Fig. 107. Another specimen two hours later in the irregular stage. ×70.

Fig. 108. The same specimen twenty hours later. ×70.

Fig. 109. *Leptogorgia* two days old. ×70.

PLATE 56.

Fig. 110. The same, three days. ×110.

Fig. 111. The same as last under compression showing ectoderm and stomodæum, *st.* ×110.

Fig. 112. The same, four days old. ×110.

Fig. 113. The same, eight days; recently attached to bottom. ×50.

Fig. 114. Two larvæ united together. ×50.

Fig. 115. The same, eleven days. At *a* is the posterior thickened region which secretes the axis. ×50.
Fig. 116. The same individual, twelve days. ×50.
Fig. 116*a*. Part of wall of body more highly magnified to show spicules in ectoderm.
Fig. 117. The same, thirteen days. Mesenterial filaments well developed. ×50.
Fig. 118. Section through *Leptogorgia* embryo of six hours. ×160.
Fig. 120. Section through *Renilla* embryo of about four hours. ×290.

PLATE 57.

Fig. 119. Section through *Renilla* embryo of four and three-quarter hours.
Fig. 121. Section through an embryo of eight and a-half hours. ×290.
Fig. 122. Portion of a section of same stage more highly magnified. ×880.
Fig. 123. Same as last. ×880.
Fig. 124. Yolk cells from last with deutoplasm spherules. ×880.
Fig. 125. Longitudinal section through embryo of twenty-two and a-half hours. ×195.

PLATE 58.

Fig. 126. Portion of same more highly magnified. ×350.
Fig. 127. Part of a section through a twenty-five-hours' embryo. ×350.
Fig. 128. Longitudinal section through a twenty-nine-hours' embryo. ×165.
Fig. 129. Part of the same more highly magnified. ×350.
Fig. 130. Part of section through a fifty-two-hours' larva. ×350.
Fig. 131. Part of section of a twenty-eight-hours' embryo to show proliferation of ectoderm. ×350.
Fig. 132. Part of section through an embryo further advanced than the last to show formation of supporting lamella; *a* represents a single ectoderm cell with swollen base, *b*; *b b* are the rounded bodies which have separated from the ectoderm cells; *c* is one of the rounded cells from the deeper parts of the ectoderm. ×350.
Fig. 133. Part of longitudinal section through a twenty-six-hours' embryo to show formation of supporting lamella.
Fig. 134. Longitudinal section through a forty-hours' larva to show formation of stomodæum. ×230.

PLATE 59.

Fig. 135. Longitudinal section through a forty-eight-hours' larva. ×230.
Fig. 136. Vertical longitudinal section through a fifty-two-hours' larva. ×165.

Fig. 137. Longitudinal section through a seventy-five-hours' larva. Œsophagus still closed. ×140.

Fig. 138. Similar section through a slightly later stage (100 hours). ×140.

Fig. 139. A similar section of a sixty-two-hours' embryo; the œsophagus has just broken through. ×140.

Fig. 140. Longitudinal section of seventy-five-hours' larva. Mouth fully formed, but "œsophageal plug" (*pl.*) still adhering to the edge of one of the septa. ×140.

Fig. 141. Sixty-hours' larva. Mouth breaking through bottom of stomodæum. ×140.

Fig. 142. Transverse section through anterior part of forty-eight-hours' larva. ×315.

PLATE 60.

Fig. 143. Transverse section from same specimen further back at the level of lower end of œsophagus. ×315.

Fig. 144. Transverse section through anterior part of a four-days' larva. ×315.

Fig. 145. From same larva at lower end of œsophagus. ×315.

Fig. 146. Transverse section of four-days' larva posterior to œsophagus. ×350.

Fig. 147. Part of a transverse section through a forty-eight-hours' larva showing a septum and general histology. ×880.

Fig. 147*a*. Portion of ectoderm from last. ×880.

PLATE 61.

Fig. 148. Section through lateral attachment of peduncular septum to body-wall. Forty-eight hours. ×350.

Fig. 149. Section through radial septum and part of body-wall. Forty-eight hours. ×350.

Fig. 150. Longitudinal section through posterior part of body of a forty-hours' larva to show formation of peduncular septum. ×135.

Fig. 151. Transverse section through posterior part of a forty-eight-hours' larva showing peduncular septum. ×315.

Fig. 152. Transverse section through the free-edge of the peduncular septum. Forty-eight hours. ×180.

Fig. 153. Part of longitudinal section through peduncular septum, highly magnified, to show axial cells. ×350.

Fig. 154. Transverse section in front of peduncular septum. Forty-eight hours. ×315.

Fig. 155. Longitudinal section just above peduncular septum. ×220.

Fig. 156. Transverse section through peduncular septum at its attachment to the body-wall. Forty-five hours.

PLATE 62.

Figs. 157, 158, 159. Longitudinal sections through 100-hours' larvæ showing continuity of stomodæal ectoderm with the mesenterial filaments. ×140.

Figs. 160, 161. Surface views of four-days' larvæ to show muscular fibres. ×880.

Fig. 162. Transverse section through the dorsal median tract of longitudinal muscles. Four days. ×880.

Fig. 163. Transverse section through ventral median tract of longitudinal muscles. ×880.

Fig. 164. Corresponding section through a younger specimen. ×880.

Fig. 165. Transverse section through septum and a septal tract of longitudinal muscles. ×880.

PLATE 63.

Fig. 166. Transverse section through septal tract below the septum.

Fig. 167. Transverse section through body-wall and peduncular septum to show longitudinal muscles in the ventral side of the latter.

Fig. 168. Part of longitudinal section through the body-wall showing the circular muscles. ×880.

Fig. 169. Transverse section through body-wall showing circular muscles in longitudinal section. ×880.

Fig. 170. Various forms of myoblasts from the entoderm. ×700.

Fig. 171. Cells from the deeper layers of the ectoderm with spicules developing in their interior. ×700.

Fig. 172. Entoderm cells with spicules in course of formation. ×700.

PLATE 64.

Fig. 173. Section through a four-days' larva passing through one of the buds (p^1.). ×315.

Fig. 174. Similar section passing through bud at p^1.; *a*, lateral forward extension of peduncular septum. ×315.

Fig. 175. Transverse section through four-days' larva passing through both buds. ×315.

Fig. 176. Ventral view of four-and-a-half-days' young polyp. ×56.

Fig. 177. The same specimen one day later from the left side. ×56.

PLATE 65.

Fig. 178. Young polyp of about nine days from right side. ×30.

Fig. 178^a. Tentacle. ×45.

Fig. 178^{b}. Bud in profile view. ×90.
Fig. 178^{c}. Bud from above. ×90.
Fig. 179. Right lateral view of part of a somewhat older polyp. ×45.
Fig. 180. Dorsal view of last. ×45.
Fig. 181. Dorsal view of polyp with recently developed exhalent zooid. ×30.
Fig. 182. Dorso-lateral view of polyp with two pairs of buds. ×30.
Fig. 183. Lateral view of polyp with third pair of buds just appearing. ×40.
Fig. 183^{a}. Dorsal view of peduncle partly contracted to show bands of circular muscles.
Fig. 183^{b}. Upper view of bud p^3.
Fig. 183^{c}. Same bud in lateral optical section.
Fig. 184. Ventral view of part of polyp with three pairs of buds. ×40.
Fig. 184^{a}. Oral view of p^1.

PLATE 66.

Fig. 185. Dorsal view of young colony having five pairs of buds and three zooids. ×40.
Fig. 186. Dorsal view of part of young colony with seven pairs of lateral buds and three pairs of zooids. ×60.
Fig. 187. Dorsal view of fully expanded colony with twelve pairs of lateral buds and numerous zooids. ×30.
Fig. 188. Dorsal view of colony in a state of contraction with thirteen pairs of lateral buds. ×30.
Fig. 189. Dorsal view of left half of the disc of a young colony. The zooids have multiplied to form groups represented by small circles. ×15.

PLATE 67.

Figs. 190 to 193. Series illustrating development of calyx-teeth. From a mature colony. ×20.
Figs. 194 to 203. Series illustrating the multiplication of a single primary zooid (*p.*) to a group of eighteen. ×80.
Fig. 204. Ventral view in optical section of the bases of the first two pairs of lateral buds to show the partition between them and its free-edge (*fl.*) below. ×50.
Fig. 205. Ventral view in optical section of an older colony to show further development of the lateral folds (*fl.*). ×50.
Fig. 206. Similar view of a still older specimen in which the two folds have met to form a single fold beneath the peduncular septum. ×50.
Fig. 207. Similar view of older specimen in which the closure of the ventral canal is well advanced. ×50.

XXV. *On the Continuity of the Protoplasm through the Walls of Vegetable Cells.*

By WALTER GARDINER, *B.A., late Scholar of Clare College, Cambridge.*

Communicated by W. T. THISELTON DYER, *C.M.G., F.R.S.*

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[PLATES 68–70.]

In Professor SACHS' latest publication the following remarkable passage occurs:* "Every plant, however highly organised, is fundamentally a protoplasmic body forming a connected whole, which as it grows on, is externally clothed by a cell membrane, and internally traversed by innumerable transverse and longitudinal walls." The above statement, both as being the outcome of pure physiological thought, and invested as it is with the authority of so distinguished a botanist, cannot fail to be very striking, on account of its forcible suggestiveness, and any observations which demonstrate an actual continuity in organs of large extent, must be of interest to show the truth of SACHS' remarks in a sense somewhat more literal than his own.

At the time of writing, the instances of the existence of any such continuity of the protoplasm were but few. SACHS† himself in 1863, and HANSTEIN‡ in the following year, had proved that in sieve-tubes an actual perforation of the sieve plate did take place, and that by means of the sieve-pores a connexion between the contents of neighbouring cells was established. Their results in this direction were fully confirmed by WILHELM,§ JANCZEWSKI,‖ and RUSSOW.¶

But it was not until the year 1880 that any further steps were made, when TANGL** demonstrated that in the ripe endosperm cells of *Strychnos Nux-vomica*, *Phœnix dactylifera*, and *Euterpe oleracea* the cell-walls were perforated by fine protoplasmic threads. His observations were in the main confirmed by STRASBURGER,††

* 'Vorlesungen über Pflanzen-Physiologie,' p. 102.

† SACHS' 'Flora,' 1863, p. 68.

‡ HANSTEIN, 'Die Milchsaftgefässe.' Berlin, 1864, p. 23.

§ 'Zur Kentniss des Siebröhrenapparates Dicotyler Pflanzen.' Leipzig, 1880.

‖ 'Études comparées sur les tubes cribreux.' Cherbourg, 1881.

¶ 'Sitzber. Dorpater Naturf. Ges.,' April 23. Also in the same journal, 1882, pp. 257–327.

** "Ueber offene Communication zwischen Zellen des Endosperms." PRINGSHEIM's 'Jahrbücher für Wiss. Bot.,' vol. xii., 1880.

†† 'Bau und Wachsthum,' p. 23, *et seq.*

whose general results in connexion with the mode of formation of the cell-wall had impressed him so strongly that the relations existing between the protoplasm and the cell-wall were of the most intimate kind, that he had devoted a special chapter in his work to the consideration of the probability of the perforation of the cell-wall by protoplasmic threads.* In this chapter he distinctly states that although he had not himself been able to establish the existence of any general continuity between vegetable cells, yet that he had but little doubt that such a relation did actually occur.

In a preliminary note published in the 'Quarterly Journal of Microscopical Science' for October, 1882,† I stated that I had succeeded in demonstrating that the continuity of the protoplasm of adjacent cells in the pelvinus of *Mimosa pudica* was maintained by protoplasmic filaments which passed through pits in the cell wall, and later on‡ I showed that the same occurs in *Robinia* and *Amicia*.

Subsequent to the publication of my first results, and previous to the present communication, appeared a most important paper by Russow.§ In this paper the author states that in the bast-parenchyma cells, and in the phlœm medullary-ray cells of many of the Amentaceæ, *e.g.*, *Populus*, *Salix*, *Quercus*, *Betula*, *Corylus*; in *Fraxinus*, *Syringa*, *Olea*, *Æsculus*, *Acer*; in the *Abietineæ*, and further in *Cucurbita pepo* and *Lappa tomentosa*, a treatment of thin sections with Chlor. Zinc Iod. demonstrates that a communication between adjacent cells is established by means of pits, the pit membrane being perforated by fine protoplasmic threads.‖

In the following paper I propose to deal more fully than I have hitherto done with my researches upon pulvini; to treat of the methods I employed, and also to give an account of my investigations as to the structure of endosperm cells, which were undertaken with the view of controlling my results with pulvini. I think that these investigations will succeed in proving not only that perforation of the cell-wall by protoplasmic threads does actually take place, but also that such perforation is of very frequent occurrence.

Methods.

Preservation of material.—As it was a point of primary importance that the material for an investigation of this kind should be preserved with the least possible change, I instituted a number of experiments with the view of ascertaining which of the various reagents commonly in use was the most reliable and what precautions were necessary to insure the most successful result.

* *Loc. cit.*, 'Die Wegsamkeit der Zellhäute,' p. 246, *et seq.*

† Gardiner, "Open Communication between the Cells in the Pulvinus of Mimosa pudica."

‡ Proc. Roy. Soc., November 11, 1882.

§ 'Sitzber. d. Dorpater Nat Gesellsh.,' 1882, p. 350. See Strasburger's remarks, 'Sitzb. d. Niederrh Ges.,' December 4, 1882. I now find (Jan. 16th, 1884), that Russow's paper was read at the January meeting of the Dorpat Society.

‖ With Frommann's and Elsberg's results I have already dealt. See 'Quart. Jour. Micr. Sci.,' April, 1883. Gardiner "On some Recent Researches on the Continuity of the Protoplasm through the Walls of Vegetable C lls."

In my paper "On the Continuity of the Protoplasm in the Motile Organs of Leaves"* I stated that when the plasmolytic condition is induced in a cell, the contracted primordial utricle does not lie free in the cell cavity, but is connected to the cell-wall by numerous fine threads of protoplasm. Since these threads are exceedingly thin and easily ruptured, the value of a preservative agent can be readily tested by observing with what degree of success it can fix the protoplasm of such a cell, and can preserve unbroken the delicate threads. (See Plate 70, figs. 34, 35, 36, and 37.)

For this purpose thin transverse sections of the pulvinus of *Robinia pseudacacia* were rapidly cut in water, and treated for about five minutes with a 10 per cent. solution of sodium chloride. The excess of salt was quickly washed out with water, and the sections were exposed in a watch-glass with frequent stirring to the action of the fluid to be experimented upon, mounted and examined.

The following are the principal results of those experiments:—

With absolute alcohol all the threads were broken, great contraction taking place, attended by great alteration in the shape of the rounded central mass of protoplasm, which now assumed an irregular as opposed to a regular spherical form with a smooth contour.

With 1 per cent. osmic acid in the same way the sharply rounded contour gave place to an irregular, uneven outline, and general swelling of the protoplasm occurred. All the strings were broken. The nucleus, however, was well preserved, though somewhat swollen. It is possible that either a stronger solution of the acid or osmic acid vapour would be more successful.

One per cent. chromic acid, with the exception perhaps of an alcoholic solution of corrosive sublimate, gave the least satisfactory results. None of the threads were preserved, and the nucleus and protoplasm had undergone great alteration of form.

A saturated watery solution of picric acid, on the other hand, gave very satisfactory results indeed. With this reagent the nucleus was especially prominently brought into view, and the protoplasm had undergone the least change. Though in many cases obvious shrinking was produced, yet as a rule the rounded contour was well preserved, and many threads remained unbroken (see Plate 70, fig. 38). Silver nitrate after plasmolysis with nitre, and gold chloride were also tried, but with little success.

As a result of these experiments it would appear that none of these reagents are entirely successful. In every case the protoplasm, even if killed at once, undergoes more or less shrinking, attended with great alteration of form. My results as to absolute alcohol agree with those of FLEMMING, who also finds that saturated picric acid, and 1 per cent. chromic acid, are preferable fixing agents for nuclear investigation. As to chromic acid our results differ. But whatever the reagent used, it is quite apparent that it is easier to deal with young cells, full of protoplasm, with very

* Proc. Roy. Soc., November 11, 1882.

small vacuoles, or no vacuoles at all, than with large full-grown cells when large vacuoles are present.

In the latter case there is every opportunity for contraction, and there is moreover always a tendency to a dilution of the fixing fluid by the cell-sap. This being the case, any successful results with full-grown cells may be regarded as very favourable evidence for the efficacy of the reagent employed. In order to eliminate any doubt as to whether the salt solution influenced the result, analogous experiments were made with fresh tissue. The great drawback to the thorough efficiency of picric acid is that it wets the tissue with some difficulty and only penetrates after some time. This fact becomes very apparent when large pieces of tissue are used at any time of difficult permeability attendant on peculiar histological structure. A saturated solution of picric acid in absolute alcohol to some extent obviates this difficulty, but it is not so successful as a saturated watery solution, although it appears to be a valuable reagent for ordinary work.

With regard to other manipulative details, it is, as mentioned above, important to cut up the material into small pieces, and also to place it at once upon cutting in the preservative medium. My usual plan, in fact, was to cut off the pulvini and allow them to drop, then and there, into picric acid, in order to avoid any loss of water due to evaporation, which as far as delicate investigations are concerned will soon very gravely affect the whole cell-equilibrium. After treatment with picric acid for about 24 hours the material is removed, rapidly washed with water, and placed in alcohol, the latter being changed until the yellow coloration of the picric acid is no longer obtained. Any method of preservation is, however, very imperfect. Not only is appreciable contraction produced, but a great amount of rigidity of the protoplasm occurs due to coagulation and death. These considerations and results determined me to use fresh material, which I employed afterwards all through the investigation.*

* In connexion with the experiments upon fresh material the results obtained with Spirogyra are of some interest. They confirm those alluded to in the text. Absolute alcohol was shown to be an utter failure. Watery picric acid was the best reagent, preserving the lenticular form of the nucleus, and demostrating the threads going to the chlorophyll bands with great success. A saturated solution of picric acid in absolute alcohol is to be preferred next, but it causes definite shrinking. The great point, however, that these experiments made evident was that throughout the entire process of preservation and staining it is necessary to keep all the solutions as nearly as possible of the same density and to avoid any rapid diffusion. Thus if it be required to put up a preparation of Spirogyra, one can first fix the cell with saturated watery picric acid. Then wash in dilute alcohol and stain with either dilute ammonia-hæmatoxylin or a dilute alcoholic solution of one of the aniline dyes. Any dense staining solution will at once cause shrinking. But after this point comes the difficulty. Dilute or strong glycerine will at once cause great shrinking, whatever be the precautions employed, and the only way which is apparently left open to adopt is to mount in such a medium as camphor water, which will cause swelling, in a dilute solution of potassium acetate or calcium chloride, or, still better, in dilute alcohol. To the latter there is the obvious objection that it will act upon most of the varnishes that are used to surround the cover glass and so work its way out. I should suggest as a varnish in this case, a strong solution of gelatine in glacial acetic acid, but hitherto I have not been able to try whether it would work. These results are, however, worth consideration.

Method of preparation.—Experiments have shown that in order to demonstrate in the most satisfactory manner the perforation of the cell wall by protoplasmic threads, it is usually necessary that the wall should be either swollen or dissolved.

Both these methods have already been successfully made use of in the case of sieve tubes by SACHS, who employed, as his reagent, strong sulphuric acid; and by HANSTEIN, who used Chlor. Zinc Iod. In both cases iodine served as a stain for the protoplasm. In investigating the subject of protoplasmic continuity, I have made use of both these methods, but with important modifications. Sulphuric acid is naturally by far the more powerful: strongly swelling or dissolving the cell wall, and laying bare, as it were, the protoplasm to the action of staining reagents, while Chlor. Zinc Iod., on the other hand, when possible, is always preferable, on account of its less vigorous action, attended with less distortion of relative arrangement.

The method used by SACHS for demonstrating the actual perforation of the sieve-plate is essentially based upon the difference of reaction of strong sulphuric acid towards the cell-wall and the protoplasm. The former is partially dissolved, or excessively swollen, while the latter remains but little acted upon, and can be readily stained and examined. The usual plan has been to mount a thin section of tissue in dilute iodine solution, and when sufficiently stained, strong sulphuric acid was run in, and the observation was made. Or the section was first stained with iodine, and then mounted in sulphuric acid. But there are some objections to this method. First, the sulphuric acid is run in, once for all, and thus its action cannot be regulated. Secondly, the iodine from its very colour is not a sufficiently deep stain. Further, the cellulose blue produced; the precipitation of the iodine; and the rapid disintegration of the tissue due to the powerful action of the acid; cause the method to be only satisfactory in such cases as sieve-tubes, where the continuity is pronounced and the material favourable, for here the cell-walls easily dissolve, and the middle lamella is but little developed.

The modification I have adopted has been to divide the process into two parts, and to substitute aniline colours for the iodine. I propose to give a detailed account of the whole process.

A thin section of fresh material is taken up on a platinum spatula; the water is removed with blotting-paper, and a drop of strong sulphuric acid is dropped upon it by means of a glass rod. When the acid has been allowed to act for a determinate time (some seconds), depending on the nature of the tissue and the extent to which the action is required to be carried, the section is rapidly washed by immersing the spatula in a quantity of water contained in a large watch-glass, at the same time stirring, so as to wash out the acid as quickly as possible, and stop its action. Thus the sulphuric acid can be kept entirely under control. After about two changes of water the section may be at once stained, or put into alcohol for future use.

The length of time that the acid requires to act naturally varies with the nature of the material used. Thick-walled tissue requires longer treatment than thin-walled,

and the permeability and peculiar characteristics of the cell-wall in question must be taken into consideration; the difference of reaction being in different cases very great. If, however, the action be properly regulated, the cell-wall will be much swollen; the protoplasm will undergo a certain amount of contraction, but, at the same time, will not be withdrawn from the cell wall at those points where any intimate union exists between the wall and the protoplasm. The middle lamella will, of course, not be destroyed. If the action be allowed to proceed further, the protoplasm itself will be attacked, the cell-wall will begin to dissolve, the middle lamella will also swell; and when in this condition will stain very deeply with reagents, thus making any satisfactory observation impossible.

Experiment shows that unless the action is decidedly forced, the cell wall, though apparently dissolved, does not in reality undergo complete solution, but is only swollen and diffluent. That this is the case may be proved by treating a washed out section with Chlor. Zinc Iod., when the ordinary blue cellulose reaction will be obtained.

The probable action of the sulphuric acid upon sections of the fresh material may now be dealt with. In the first place, the protoplasm is apparently at once killed, although, at the same time, decided shrinking occurs, owing to the great dehydrating power of the reagent. This shrunken appearance is, however, somewhat magnified, because, in addition to the contraction produced by the rapid abstraction of water, the protoplasm has also been squeezed and pressed upon, on all sides, by the swelling cell-wall. But the point which must be especially strongly brought into prominence, is the fact that during the swelling any close relation which may exist between the protoplasm and the cell-wall appears to be maintained, at least where such relation is at all pronounced. Thus in cases where reactions with Chlor. Zinc Iod. and iodine show that the closing membrane of a pitted cell is perforated by fine protoplasmic threads, it will be found that when such a cell is treated with sulphuric acid, the protoplasm projecting into the pit, and especially that portion of it abutting on to the closing membrane, will firmly adhere to the latter, and will resist, without rupturing, a very considerable strain; and even if rupture should at length take place, it will seldom, if ever, occur close to the pit membrane. In attempting to explain the appearances produced by the action of strong sulphuric acid, one must clearly bear in mind that there are two factors to be considered, viz.: the rôle of the protoplasm and the rôle of the cell wall. At the same time there is going on, not only a shrinking of the one, but a swelling of the other. Two principal objections may be very reasonably brought forward to explain the fact, that the protoplasm adheres to the pit. First, it may be said, that the protoplasm is retained and even injected into the pit by the pressure of the swelling wall. That this objection will not hold is apparent from the fact that the same phenomenon occurs in the case of cells which have been cut into. Furthermore, the swollen wall frequently does not abut directly on to the protoplasm, but a considerable space intervenes between the two. Again, by the action of strong

dehydrating agents a further shrinking of the protoplasm may be induced. The second and more important objection is, that the narrowing of the pit, on account of the swelling, imprisons and firmly embraces the protoplasm in the pit cavity. In answer to this, it may be urged that the shrinking of the protoplasm takes place more quickly than the swelling of the wall, and that the protoplasm projecting into the pit would have time to withdraw before being imprisoned. In deep pits of small diameter, it is indeed possible that the narrowing of the cavity does play some definite part, but whether this be so or not, experiment proves that the protoplasm also adheres to pits which are shallow, and moreover possess sloping sides. In this case, any such explanation could hardly be brought forward. Lastly, it must be remembered that the action of the sulphuric acid is carefully regulated, and is not carried to an extreme limit, and that the results obtained with this reagent have been fully confirmed with Chlor. Zinc Iod. All the preceding remarks as to the action of sulphuric acid apply only to the cases in which fresh material is used, since here the protoplasm has not been rendered brittle by any preliminary treatment with reagents, and consequently has undergone as little alteration as possible, and will not break when any slight tension is set up.

After treatment with sulphuric acid, and washing out with water, the section may be stained with iodine, as in the usual process; but I used in preference, and with greater success, analine dyes, especially the violet and blue.

In my earlier experiments I used HOFMANN'S violet (*Trimethyl rosanilin*) as the staining reagent. In the first place, HOFMANN'S violet is a dye which, of all others, is extremely rapid in its action, quickly and thoroughly permeating the tissues. Again, it works extremely well with sulphuric acid, being soluble in, and hardly affected by this reagent, as far as all its staining properties are concerned. Thus one need not take such care to wash out the acid before staining; for, although when the proportion of acid is large the HOFMANN'S violet is temporarily turned green, yet on subsequently washing with water before mounting in glycerine, the violet colour is restored. The whole process may, indeed, be done in one operation, for the solid dye may be dissolved in strong sulphuric acid; the mixture furnishes a dark brown-yellow solution. The section is now simply treated with the mixture, and then washed well with water. The above method gives extremely satisfactory results with sieve-tube preparations; and, moreover, any lignified tissue which happens to be present is coloured gold yellow, as in the ordinary aniline sulphate reaction.

To the use of HOFMANN'S violet there is, however, the great objection that the whole of the tissue—protoplasm, cell-wall, middle lamella, and pit-membrane—is stained. If, however, the stained section be treated for some long time (three to four days), with dilute glycerine the dye in the cell-wall, middle lamella, and pit-membrane dissolves out, whereas that staining the protoplasm remains but little acted upon. This lengthy manipulation is an obvious objection, but nevertheless HOFMANN'S violet often gives extremely satisfactory preparations, and by mounting the section in

strong glycerine, the middle lamella may be made almost transparent; and when in such a condition will no longer present any hindrance to successful observation.

But the better and more reliable reagent is HOFMANN'S blue.* As a result of numerous experiments I am able to state that this dye is a particularly satisfactory reagent for staining the protoplasm alone, and as such is of extreme value for botanical research, and supplies a long-felt want. I find that it works best after treatment with picric acid, and that unless the solution in alcohol be too strong or the staining be decidedly forced, there will be little if any coloration of structures other than protoplasm. But when HOFMANN'S blue is used, the washing-out of the sulphuric acid must be carefully attended to, for the two will not work together as in the case of HOFMANN'S violet. After staining, the section is well washed with water and mounted in dilute glycerine. Such was the method I used in my investigation upon the structure of pulvini. Having thus dealt at some length with sulphuric acid, I must now proceed to describe in the same way Chlor. Zinc Iod.

The action of this reagent is well known. It causes a swelling up of the cell-wall, and at the same time colours the cellulose blue. It is, however, much less violent in its action than sulphuric acid, causing but little distortion of form or displacement of relative arrangement. There is simply a slow and regulated swelling. Sections may be at once treated with Chlor. Zinc Iod., or may be first stained with iodine which helps as it were to accentuate its differentiating powers. The easy manipulation attending the use of Chlor. Zinc Iod., its high refractive index, and the satisfactory manner in which its gradual action may be observed, cause it to be one of the most valuable reagents employed in botanical research. For the demonstration of the presence of protoplasmic threads running through the thickness of the cell wall. TANGL† first used Chlor. Zinc Iod. in his investigation upon the endosperm cells of *Strychnos*, *Phœnix*, and *Areca*. The sections were first stained with iodine and then

* Under the somewhat loose term aniline blue, are frequently included and described by writers a number of salts which are obviously perfectly distinct, both as regards chemical and physical characters. For example, there is soluble or water blue, insoluble blue, gentiana blue, phenylene blue, benzyl blue, methylene blue, cyanine or chinoline blue, HOFMANN'S blue, besides others, Bavarian blue, Capri blue, &c., some of which are patented products of the various aniline-dye manufacturers. Frequently any given dye obtained from one maker will absolutely differ in staining properties from that of the same name obtained elsewhere. This being so, it is necessary to state very clearly the exact name and maker of any of the so-called aniline blues that may be made use of. I first used HOFMANN'S blue at the Würzburg laboratory, and to the kindness of Professor SACHS I am indebted for the information that it is known as HOFMANN'S blau (anilin blau), and may be obtained from MORELLI, Druggist, &c., Semmel Straase, Würzburg. A tolerably strong solution is made in 50 per cent. alcohol, to which is added a drop or two of acetic acid. After staining, the section is washed with water and mounted in dilute glycerine or glycerine jelly. I find that when dyes are dissolved in solutions containing a higher percentage of alcohol than that named above, most dyes will lose their selective power for particular structures, and will begin to stain all tissues alike. These results are confirmed as regards animal tissues by Dr. MAYER, of the Naples Zoological Station. See Mt. Zool. Stat., Neapel ii. (1880), pp. 1–27.

† *Loc. cit.*

mounted in Chlor. Zinc Iod. The cell-wall is coloured yellow; the protoplasm and the protoplasmic threads a dark brown. The success of the reaction depends upon the fact that when cellulose has experienced a loss of water, and has become dry as in the case of ripe endosperms and other dry tissues, the Chlor. Zinc Iod. will not at first give the usual blue coloration. It is only after some considerable time that the section will begin to turn blue, or if the cell-wall be very thick or very dry, the blue colour may not be produced at all, but only a yellow brown, which is frequently increased in depth by the precipitation of iodine attending such lengthy action. Sections of a germinating seed of *Phytelephas* furnish an excellent proof that the assumption of the blue colour on treatment with Chlor. Zinc Iod. depends upon hydration, for whereas the normal cells will give a yellow colour, those which are being encroached upon by the absorbent foot of the growing embryo, and are being broken down and at the same time thoroughly wetted, will give in a peculiarly characteristic manner the customary blue cellulose reaction.

But usually in sections of ripe endosperms the cell walls become yellow, and the protoplasm colours dark brown. In most cases nothing can be seen at first of any threads in the cell-wall, but after some time (varying from a quarter of an hour to one hour) they gradually come into view and are moreover apparently increased in size by the gradual precipitation of iodine upon them due to the action of the Chlor. Zinc Iod.

One great objection to this method is that when fresh tissue or thin walled tissue is used, the ordinary blue cellulose reaction occurs which totally obscures the threads from view, and makes all observation of no avail. Moreover, no permanent preparations can be made. My first idea was to employ the same modification as I had adopted in the case of sulphuric acid and use HOFMANN'S blue instead of iodine. With this, however, I at first experienced some difficulty. TANGL* found in *Strychnos* that when he had swollen the walls with water and could see the threads with dilute iodine solution, he was unable to stain them with any ordinary dye, such as hæmatoxylin or carmine. In the same way I found that after the action of iodine and Chlor. Zinc Iod. I could not succeed in staining the threads with any solution of aniline colours. In consequence of this I made a number of experiments with *Strychnos*. I found that although no dyes would demonstrate the threads, yet with solutions of such coloured bodies as gold chloride, picric acid, chromic acid, and iodine, they became more or less clearly apparent. It will be noticed that all these substances are well-defined crystalloids, whereas most of the aniline colours are inclined to be colloidal or, at least, are crystallised with some difficulty. This suggested that the whole phenomenon was simply a matter of diffusion, the solutions of crystalline bodies apparently permeating the substance of the cell wall (crystalloid), but especially diffusing into the protoplasm (colloid), and in the same way the solution of the colloidal aniline dyes diffusing but little or not at all into the colloidal protoplasm. In consequence of this conclusion I made the experiment of dissolving the solid HOFMANN'S

* *Loc. cit.*

blue in a 50 per cent. alcoholic saturated solution of picric acid, under the supposition that the latter might mechanically carry with it into the tissue the dissolved aniline dye, and that on washing out the picric acid with water, the protoplasmic threads would be left stained. Such treatment I found to be perfectly satisfactory, the threads running through the cell-walls and, indeed, the whole of the protoplasm being stained blue, while the cell-wall either remained quite uncoloured or, if the action was forced, coloured but slightly, and to a much less extent than the protoplasmic threads which could still be easily recognised.

As regards the action of picric acid, experiment seems to show that in addition to being one of the most valuable preservative media, it also restrains the coloration of the cell-wall by solutions of such a dye as HOFMANN'S blue, which though a special stain for the protoplasm, will upon lengthy action stain the cell-wall also. Thus, if two sections be stained, one of alcohol material and the other of material which has been treated with picric acid previous to preservation in alcohol, in the former the cell-wall will be definitely stained, while in the latter little, if any, coloration will occur. Thus, the action of the picric acid is of twofold significance, not only serving as a vehicle for the passage of the HOFMANN'S blue into the minute protoplasmic filaments, but also restraining at the same time the coloration of the cell-wall.

It now only remains for me to describe in detail my method of manipulation with Chlor. Zinc Iod. and the picric acid solution of HOFMANN'S blue. Sections of fresh material are cut in water and placed in ordinary iodine solution until they are well stained. They are then taken out by means of a platinum lifter, the iodine solution is removed with blotting paper, and they are mounted in Chlor. Zinc Iod. In those cases where the blue colour is not produced until after some time, it is usually possible to see something of any threads that may be present, and thus many very conclusive observations may be made prior to staining with picric-HOFMANN'S-blue. In fact, treatment with iodine will often bring out clearly many points that HOFMANN'S blue will not, such as a satisfactory demonstration of the passage of the threads through the substance of the middle lamella, where the lamella is well developed. Further, the threads appear thicker than with HOFMANN'S blue, and in any case the treatment will give some idea of what one may expect to see after staining with the aniline dye. The time that Chlor. Zinc Iod. requires to act depends greatly upon the character of the tissue. With many dry endosperms and other cells with thickened walls it will take as long as twenty-four hours to thoroughly permeate the tissue. In my own experiments I was in the habit of mounting in Chlor. Zinc Iod. on one morning and staining on the following day. If not allowed to act for a sufficiently long time, it will be found that while some portions of the walls are swollen, others are hardly acted upon, and that the difference of refractive index of these two portions will give a very confusing appearance to the whole section, and very greatly hinder successful observation. Experiment alone can decide the time required for the complete action;

the only point of importance requiring attention is that the reagent should be allowed to act long enough.

After treatment with Chlor. Zinc Iod. the section is well washed in water until the blue or brown colour (as the case may be) has disappeared. It is then placed for about a quarter of an hour in the picric-HOFMANN'S-blue solution, and after being well washed is mounted in glycerine or glycerine jelly.

As before mentioned, the staining solution is made as follows: To 100 cub. cent. of strong alcohol (*e.g.* about 90 per cent. strength) is added an equal bulk of distilled water. The resulting solution is saturated with picric acid, and HOFMANN'S blue is added, until the liquid is of a dark blue-green colour. It is then filtered.

I used the method with Chlor. Zinc. Iod. almost entirely in my researches upon the structure of endosperm cells. I did not discover the picric-HOFMANN'S-blue modification until I had finished my work with pulvini. Thus, the results with pulvini rest mainly on the sulphuric acid modification.

On the nature of the pit membrane.

If a thin section of almost any tissue be treated with Chlor. Zinc Iod. it will be seen that the walls of almost every cell are distinctly pitted.* These pits are brought into prominence from the fact that whereas the thicker unpitted portions of the cell wall give a well-defined cellulose blue reaction, the thin pit-closing membranes stain but slightly, or in some cases apparently remain quite colourless.† Indeed, so common is this pitting, which the above-mentioned reaction demonstrates, that it would be a statement little short of the truth to say that every cell whatsoever, is pitted to a greater or less degree. Moreover, the closing membrane of the pit itself may also be pitted, as in the seed of *Lupinus hirsutus*, &c. As a rule, it is only in the case of thin walled cells that it is necessary to apply any reagent to bring this pitting into view, for the more the cell wall increases in thickness the more pronounced does the pitting become, until its appearance is at length so marked that we are accustomed to speak of it as a pitted cell *par excellence*. It is a point of special interest to note that

* Cells of *Strychnos*, *Dioscorea*, and *Tamus* are notable exceptions.

† Even in cases where an *en face* view of the pit will give the impression that no coloration has occurred, a transverse section will show that in reality it is slightly stained, and contrasts as markedly with the deep blue stain of the thick wall as the same blue staining of a young cambium cell does with that of the mature, full-grown cell which is subsequently produced. The pits in the parenchymatous cells of the petiole of *Cycas revoluta* are of special interest here. There are, as it were, two systems of pits. The larger, which are arranged in rows up the sides of the cell, face the intercellular spaces, and stain deep blue with iodine and Chlor. Zinc Iod. The smaller pits between the communicating cell walls, on the other hand, do not stain perceptibly when viewed from above. (See Plate 68, fig. 12.) DE BARY mentions pits of *Cycas* and *Encephalartos* which give a callus reaction. (See 'Verg. Anatomie,' p. 125. See also RUSSOW'S important paper, "Ueber Tüpfelbildung," &c. Sitzber. der Dorpat Natur., 1882, pp. 350-389. Russow is inclined to think that no staining of the pit membrane occurs.)

in two adjoining cells * any unequal thickening that may occur always takes place symmetrically on either side of the first formed cell-wall, and in such a way that the two pits which are formed in consequence are exactly opposite one another.

Among many other examples, the thickened cells of hard endosperms and the parenchymatous tissue of all pulvini exhibit this structure to a high degree, and since it was probable that by means of these pits a communication between adjacent cells was established, the study of the nature of the pit-membrane becomes one of great importance. The result of experiments with various staining reagents may now be detailed.

As at first mentioned, Chlor. Zinc Iod. usually stains the pit membrane but little.† Instead of treating the section with this reagent alone, better and more decisive results may be obtained by first soaking the tissue in iodine, then rapidly washing to get rid of the extraneous iodine which would otherwise be precipitated over the tissue, and then mounting in Chlor. Zinc Iod., or the section may be first treated with Chlor. Zinc Iod., then washed and mounted in iodine solution. This gives good results in cases where protoplasm is left sticking to the pits as in the parenchyma cells of the pulvinus of *Amicia* or the endosperm cells of *Bomarea*.

Methyl violet gives very striking, and at the same time is apt to give very deceptive results. When a washed out section of pitted tissue that has been exposed to the action of sulphuric acid is treated with this reagent the whole of the tissue becomes rapidly stained. The protoplasm is coloured a deep purple; the cell-wall is stained violet; and the closing membrane and sides of the pit are brought into prominence since they assume a purple colour, somewhat lighter than that of the protoplasm. The middle lamella also stains deeply. Now in a much-pitted tissue, *e.g.*, that of a pulvinus, the cell wall after treatment with sulphuric acid usually becomes much swollen, causing an elongation and at the same time a narrowing of the pits, and may, moreover, in its swollen condition closely invest and surround the protoplasm. When such a section is treated with methyl violet, the deeply stained tubular pits, being placed symmetrically opposite one another on either side of the common cell wall, abut on the shrunken and similarly stained protoplasm, and give the impression that a distinct and well-defined continuity exists from cell to cell. Thus in *Amicia* the most beautiful and striking appearance is produced which is further heightened by the fact that processes from the main protoplasmic mass usually go for some distance into the pits. (See Plate 68, fig. 10.) If, however, the section be treated for some time with dilute glycerine, the colour is dissolved from the cell wall and the pits and the protoplasm alone remains stained, thus making the real state of things apparent.

The reaction with methylene blue is perhaps the most characteristic. When a section is stained with this reagent before treatment with sulphuric acid, the cell wall and the pit membrane will be deeply coloured, the protoplasm being left unstained.

* I exclude from this statement such cases as that of a cell adjoining a vessel, &c. See 'Sachs's Text-book,' English edition, 1882, p. 26.

† In old cells with thick pit membranes the staining of Chlor. Zinc Iod. is, however, very apparent.

If, however, the section be first treated with the acid, then washed, and stained with methylene blue, only the closing membrane and the sides of the pits will be stained (see Plate 68, fig. 8), unless the action of the sulphuric acid be forced. Both the protoplasm and the rest of the cell-wall undergo scarcely any coloration. *Thus methylene blue, apart from its great value as a stain for cell-wall, becomes by this modification a reagent for pit membrane. Naturally HOFMANN's blue stains neither the cell-wall nor the substance of the pit membrane. The whole results of my investigation appear to point to the conclusion that the staining of this reagent is specially confined to the protoplasm. In the case of many palm endosperms, where after the action of Chlor. Zinc Iod. and picric-HOFMANN's-blue threads can be observed going through the closing membrane of the pits, it is the threads which are specially stained, and are in consequence defined from the substance of the pit membrane. Indeed, so characteristic is the staining of HOFMANN's blue, that experiment seems to point to the conclusion that in those cases where a staining of the pit membrane occurs, such staining points to the presence of protoplasm.

There is, however, another special structure which is also stained by HOFMANN's blue, and which can be distinguished from protoplasm by its solubility in strong sulphuric acid, viz.: the callus of sieve-tubes. It was RUSSOW† who first used aniline blue as a reagent for callus, and even combined it with Chlor. Zinc Iod. As I did not know what particular blue RUSSOW used, I made a number of experiments with the various blues I had at my disposal,‡ with the result that the special staining of the callus was confined to two of them, viz.: HOFMANN's blue and water or soluble blue, one of which it is pretty certain that RUSSOW employed. Water blue is only second to HOFMANN's blue in that it also especially stains protoplasmic structures. Now the properties of callus are somewhat peculiar.§ WILHELM showed that it was soluble in sulphuric acid, and insoluble in ammoniacal oxide of copper. In the former respect it resembles cellulose, and indeed its mode of formation—arising as symmetrical warts on either side of the cell wall—as described by JANCZEWSKI,‖ and confirmed by STRASBURGER,¶ certainly give some colour to this idea.** On the other hand, unlike cellulose it

* After keeping the section for a long time in dilute glycerine, staining of the protoplasm does take place since the glycerine dissolves the dye. This solution ultimately stains the protoplasm.

† RUSSOW, 'Sitzber. Dorpater Nat. Ges.,' 1881, April 23, and 'Bot. Ztg.,' 39, 1881, p. 723.

‡ HOFMAN's blue stains protoplasm and callus. Soluble or water blue, ditto. Benzyl blue, protoplasm cell-wall and callus, like rest of cell wall. Insoluble aniline blue, *i.e.*, solution in spirit, as benzyl blue. Neither of the latter appear to stain the pits. Methylene blue, stains cell-wall and pit membrane Phenylene blue resembles methylene blue. Both water blue, methylene blue, and HOFMANN's violet may be obtained at MARTINDALE's, New Cavendish Street, Portland Place, London. The rest of the dyes that I used were obtained from the Actien Gesellshaft für Anilin Fabrication, Berlin.

§ 'Beiträge zur Kentniss des Siebröhrenapparatus Dicotyler Pflanzen.' Leipzic, 1880.

‖ 'Études comparées sur les tubes cribreux.' Cherbourg, 1881.

¶ 'Bau und Wachsthum,' p. 56, *et seq.*

** This was first noted by WILHELM. *Loc. cit.*, p. 16.

is insoluble in ammoniacal cupric oxide, and moreover it gives with Chlor. Zinc Iod. not the customary blue but an intense red-brown coloration. Lastly, the result with HOFMANN'S blue appears to point to a protoplasmic character, opposed to which conclusion is the fact that it dissolves in sulphuric acid. Thus the question appears to be, whether it is related to protoplasm or to cellulose, or whether it consists of a modified cellulose basis permeated by a protoplasmic structure.* This, however, minute study of development alone can decide, but the point I wish to bring forward is the fact that it is coloured by dyes which especially stain the protoplasm.

There is a curious parallelism in the action of callus towards HOFMANN'S blue and of pit membrane towards methylene blue, after treatment with the same reagent (viz.: sulphuric acid) which may perhaps be worth mention.

If a section of a second year stem of *e.g.*, *Vitis vinifera*, be treated with HOFMANN'S blue it will be found that both the protoplasm and the callus will be stained. If, however, sulphuric acid be allowed to act before staining, the callus will naturally be dissolved and will no longer colour, and only the protoplasm will be left stained.

If in the same way a section of pitted tissue, *e.g.*, pulvinus of *Robinia*, be treated with methylene blue, both the cell wall and the pit membrane become coloured. But if the section be first treated with sulphuric acid, the swollen or dissolved cell wall will remain unstained and only the closing membrane and the sides of the pits will alone be stained blue.

Now, if it be allowed that callus may be regarded as altered protoplasm, it might be suggested from the foregoing reactions that cell wall is to be looked upon as altered pit membrane, or rather that pit membrane is to be regarded as consisting of cell wall that has retained its original properties and has undergone comparatively little chemical change. However, I prefer at present to draw no definite conclusions from these observed phenomena but merely desire to put forward the facts.†

On the structure of pulvini.

Having thus treated of the methods employed, and made some remarks as to the nature of the pit membrane, I am now in a position to proceed with the description of my investigation of the structure of pulvini. This work was commenced in the Würzburg laboratory in the month of July, 1882, under the direction, and at the suggestion, of Professor SACHS.

I studied in detail the pulvini of *Mimosa pudica*, *Robinia pseudacacia*, *Amicia*

* See RUSSOW'S observations on Abies Picta, 'Stab. d. Dorpat. Naturf. Gesell.,' 1881, p. 70. Also STRASBURGER, 'Bau und Wachsthum,' p. 60. RUSSOW ('Stab. d. Dorpat. Naturf. Gesell.,' Feb. 17th, 1882), like myself, in contradistinction to JANCZEWSKI ('Mem. de la Soc. des Sc. Nat. et Math. de Cherbourg,' vol. xxxiii., p. 209, 1882), believes that the reactions of callus point essentially to its protoplasmic nature.

† I find in reality that the above reaction of the pit membrane with methylene blue takes place in consequence of the fact that the membrane is more resistant than the rest of the cell-wall. Whether this is in consequence of the presence of protoplasm in its structure remains to be proved. This STRASBURGER also found to be the case. See 'Bau und Wachsthum,' p. 16.

zygomeris, and *Phaseolus multiflorus*. I do not intend in the present paper to enter into any discussion with regard either to the nature of irritability or the phenomena of movement of which these plants serve as illustrations, but merely to confine myself to such structural detail as is necessary for the clear comprehension and significance of my results. The principal literature of the subject has been collated by PFEFFER,* to whose researches and those of SACHS† we owe the greater part of our knowledge of what is one of the most interesting phenomena of plant life.‡

Mimosa pudica.—As a rule the main pulvini at the base of the petiole of the leaf were chiefly made use of on account of their larger size and consequent easier manipulation. The secondary and tertiary pulvini, however, gave the same result. Thin longitudinal and, as far as possible, axial sections of the fresh material were taken, since the unequal contraction and puckering-up of the tissue due to the tensions produced by the violent action was not so great as in transverse sections.

As regards its anatomical structure the pulvinus shows a thin vascular bundle surrounded by a thick layer of parenchymatous cells. The epidermis is not pronounced and the epidermal cells have undergone very little, if any cuticularisation. For the most part confined to the underside of the pulvinus are several long stiff multicellular hairs.

Immediately under the epidermis the cells are small, as are those immediately surrounding the bundle, and between these two layers occur the cells of maximum size (see Plate 68, figs. 1 and 3). From the hypodermal cells inwards the intercellular spaces, which are at first inconspicuous, become more and more apparent, until in these cells around the bundle itself a system of large communicating air spaces exist (Plate 68, figs. 3 and 4). The vascular bundle is arranged on the concentric type, the phlœm being outermost and surrounding the xylem. In the phlœm the walls of the prosenchymatous cells are greatly thickened and very highly refractive; the middle lamellæ between them are also almost inconspicuous (see Plate 68, fig. 1), the structure of which is similar to that of *Mimosa*. The cell-walls of the upper half of the pulvinus are thicker than those of the lower, which moreover is the side towards which the bending takes place, and this rule is followed in the secondary and tertiary pulvini also, viz.; that the cells of the side which becomes concave on bending, have always thinner walls than the side which becomes convex, so that whereas in the main pulvini the underside has the thinner walls, in the pulvini of the leaflets the reverse is the case. The parenchymatous cells each contain a number of chlorophyll granules and a nucleus. One or more drops of tannin are also present,§ which can be well seen,

* PFEFFER, 'Physiologishe Untersuchungen,' 1873, i. id.; 'Die periodischen Bewegungen der Blattorgane,' 1875; see also 'Pflanzen Physiologie,' 1880.

† SACHS', 'Handb. der Exp. Phys.,' 1866, p. 479, *et seq.*

‡ See also DARWIN, 'Movements of Plants,' 1880.

§ I could not detect the special pellicle mentioned by PFEFFER. See SACHS' Text-book, p. 889.

by staining the section with methyl violet, and washing with alcohol. The dye is then dissolved from everything but the tannin drops. With osmic acid they also stain a blue-black and with chromic acid a brown-yellow. The latter reagent, however, affects the protoplasm as well, and thus does not allow the individual drops to be distinguished.

On treating with Chlor. Zinc Iod. it becomes apparent that the parenchymatous cells are freely pitted, each such pit being so little stained as to appear quite transparent, thus presenting a marked contrast to the ordinary deep cellulose blue of the rest of the cell-wall. The pits, as a rule, are somewhat shallow and of small diameter except in those cells bordering on the vascular bundle, which from their peculiar configuration in consequence of the presence of large intercellular spaces exhibit on their walls pits of much larger size (Plate 68, fig. 4). The pits are greater in number on the longitudinal than on the transverse walls. The thin pit membrane between two cells is, except under very favourable circumstances, extremely difficult to observe in the unstained condition. It is perhaps brought out most clearly by staining the protoplasm with HOFMANN'S blue when the unstained wall will be seen as a thin colourless membrane separating the protoplasm of one cell from that of the other.

Even with the most favourable section there is no indication of the existence of any connexion between the protoplasm of neighbouring cells. Deep staining with iodine or with HOFMANN'S blue shows the outline of the protoplasm to be well defined and sharply limited by the cell-wall at all points.

But if the wall be swollen with sulphuric acid, and after washing stained with iodine, methyl-violet and glycerine, or HOFMANN'S blue, it will become apparent that a definite communication between the cells does exist, and that such communication is established by means of the pits (Plate 68, fig. 5). The appearance of a well-prepared section is extremely characteristic, reminding one to some extent of a gold chloride preparation of corneal connective-tissue cells. The protoplasm, as it has contracted away from the cell-wall, has adhered to the membranes of the pits, at those points in the cell-wall where pits are present; and in consequence, the whole section presents the appearance of a number of stained and interconnected irregularly-shaped stellate masses, for the narrow processes of any one mass unite at their apices with those proceeding from the neighbouring masses, thus exhibiting a well-defined reticulate arrangement. The reason that the processes proceeding from the masses of two contiguous cells are opposite one another obviously depends upon the symmetrical development of pits on either side of the cell-wall (Plate 68, fig. 3). But that the relation between two such processes is of the most intimate character is quite evident from the fact that in many instances it appears that an optical continuity exists between them, thus establishing a means of communication between cell and cell (Plate 68, fig. 5).

Successful sections are somewhat difficult to prepare, for if the sulphuric acid does not act sufficiently long, the cell-wall is either little or not at all swollen, and when in this condition cannot be permeated by the dye, and if the action has been allowed to

proceed too far, the protoplasm is attacked and the delicate connexions soon become obliterated. Moreover, at the same time the middle lamella becomes swollen and will deeply stain, which of all things is to be avoided. A regulated action of the acid gives the best results, and if the protoplasm be not sufficiently shrunk to show up the processes to the best advantage, the section need only be mounted in strong glycerine which will soon bring about the desired effect. Even in one and the same preparation, though a successful one, the acid may have acted unequally, due, it may be, to varying thickness of the section, and thus the different results produced by the acid may be observed at the same time. However, in a well-prepared section, where the action of the acid has been properly regulated, plain examples of continuity are apparent. Upon longer treatment, the further shrinking of the protoplasm causes a greater tension to be exerted upon the processes and rupture ensues. This frequently occurs, but the rupture nearly always takes place on one or both sides of the point where the thin thread-like process crosses the middle lamella, and seldom at the point itself. Thus the threads cannot be said to be merely pulled out of the pits, for rupture takes place in such a manner that a longer or shorter length still remains in the pit cavity.

Finally, when the action of the acid has been carried too far, the processes appear to have been partially destroyed, and but few can be traced as far as the swollen and now deeply-stained middle lamella. Many of the processes appear to be directly and uninterruptedly continuous from cell to cell, whilst others are swollen at the point where they cross the middle lamella. In other cases between the two ends of the strongly-stained processes there is a lighter-stained portion, which connects the two This lighter-stained area exhibits a haziness and appears to be somewhat indistinct, although well defined from the rest of the swollen cell-wall, and clear enough not to be confounded with the middle lamella (Plate 68, fig. 5). Again, when the protoplasm is but slightly contracted, and but little tension has been exerted on the threads, the point of junction of the two threads is both slightly swollen and also coloured darker than the rest. In spite, however, of the fact that in several cases direct continuity appears to exist, I am strongly of opinion, both from analogy and from such appearances as I last described, that in reality a sieve-plate arrangement occurs. It must be borne in mind that the difficulties of examination are great, both on account of the smallness of the pits and the thinness of the pit membranes, but in any case we cannot imagine that the threads go bodily through the pit, for were it so, the pits would not possess a closing membrane, and ordinary staining would soon demonstrate the existence of the protoplasm, by which the pit was perforated.

Although Pfeffer's* results appear to prove that it is the underside of the pulvinus which is especially sensitive, I have not been able to establish any difference between them as far as histological evidence goes. Nor is this to be greatly wondered at, for the method for such a discrimination is essentially rough, and one would hardly

* See Sachs' 'Text book,' p. 889.

expect such physiological differences to be made apparent by a somewhat coarse histological treatment. Certain cells occur scattered about in the tissue which are both larger and stain more deeply than their neighbours, but the latter phenomenon may be, and probaby is, caused by the presence of tannin. In the parenchyma of both the upper and lower side of the pulvinus the connexion appears to be more pronounced in the cells of the middle layer than it is in those either next the epidermis or next the vascular bundle; and since the cells are more freely pitted on the longitudinal than on the transverse walls more connexions exist through those of the one than of the other.

With regard to the middle lamella there is some difficulty, unless very careful preparation is adopted. It will in any case stain, the depth of the staining depending upon the action of the acid and of the dye, and if the treatment with the one or with the other be forced, the great coloration of the lamella will so obstruct the view that it will be impossible to see with certainty whether or not a distinct continuity of the protoplasmic processes occurs. The difficulty may, however, in a great measure be removed by long treatment with strong glycerine, which both dissolves the greater portion of the colouring matter from the lamella, and at the same time renders it sufficiently transparent for a decisive observation to be made.

The bast fibres of *Mimosa* are of peculiar interest with regard to this question. The middle lamellæ between these cells are so little developed that they are recognised with some difficulty, and which is an important fact, do not stain at all. Consequently, the additional factor of difficulty, that the presence of a well-developed middle lamella involves, is here done away with. Each bast cell is freely pitted, the pits of neighbouring cells being placed symmetrically opposite one another. When treated with sulphuric acid and stained in the usual manner the following appearance is produced. The pit membranes being somewhat thick have distinctly swollen, and in so doing have increased the distance from one another of the ends of the protoplasmic processes projecting into the pit cavity. All the processes are deeply stained, and between each symmetrically opposite pair is a small less stained portion traversing the pit membrane, which from its reactions must be protoplasm. Thus it stains with iodine, and when coloured with methyl violet is not dissolved by glycerine (Plate 68, fig. 6). It is also well brought out by HOFMANN'S blue, the staining characters of which have already been sufficiently dwelt upon. That it is not callus is clear from the fact that it does not dissolve in sulphuric acid. The structure traversing the pit membrane is somewhat difficult to observe, both on account of its very small size and its want of definition. Indeed, it rather presents the appearance of a small blue cloud between the ends of the deeply-stained and well-defined processes.

The protoplasmic processes projecting into the pits are broad at their extremities, and are at the same time more deeply coloured at that point. They gradually taper off from the bottom of the pit inwards, widening again as they join the general proto-

plasm of the cell. Each pair of processes with their above-mentioned broad ends and the cloud between them forcibly suggest a sieve-tube arrangement, and from analogy, as I shall point out later on, I believe that such is the case. I have, however, with the highest powers at my disposal been unable to resolve the stained structure traversing the pit membrane into fine lines as I had hoped to do, although the whole appearance is most strongly suggestive of a striation, the direction of which is parallel to the long axis of the pit. However, it seems certain that there is a protoplasmic communication which can be plainly seen, and is not complicated by the presence of a stained middle lamella.

Thus it appears that from the epidermal cells right up to the last living bast fibre which impinges on the first dead vessel a direct continuity from cell to cell has been established, and that such a pulvinus may be regarded as a connected whole.

Robinia pseudacacia.—As in *Mimosa*, thin axial, longitudinal sections of the main pulvini were examined. Fresh material was used in every case, and after treatment with sulphuric acid the sections were stained with either HOFMANN'S violet and glycerine, or with HOFMANN'S blue. In fundamental structure the pulvinus of this plant resembles that of *Mimosa*. Rough examinations show that it is much larger, and that its surface is quite smooth and free from hairs. The cells do not appear to be so freely pitted, nor is tannin so abundant. In many of the cells which are scattered about the tissue, and are smaller than their neighbours, are crystals of calcium oxalate, which can be well seen embedded in the protoplasm of the containing cell. The cells in certain cases possess more than one nucleus. The nuclei are large and well developed, and are brought into prominent view in the case of tissue which has been previously treated with picric acid.

After treatment with sulphuric acid it can be seen that, in a well prepared section, the cells present very much the same appearance as those of *Mimosa* (Plate 68, fig. 7). The continuity existing between the processes is not as pronounced as in the former case, and the appearance of threads going straight and uninterruptedly through the pits is not so frequent (Plate 68, fig. 7). On the contrary, there is more indication of the existence of a sieve-plate-arrangement, which is very marked in those cases which admit of successful observation. Frequently at the point of junction of two processes there is a distinct and well defined swelling which stains perceptibly lighter than the very darkly stained threads, which it connects one with the other. It can clearly be distinguished from the pit membrane and the middle lamella, and can almost certainly be resolved into a striated appearance, although the observation cannot perhaps be regarded as perfectly conclusive or perfectly satisfactory. In consequence of the presence of fewer pits on the cell walls the interconnecting protoplasmic processes are fewer in number than in *Mimosa*. The bast fibres present the same appearance as those of *Mimosa*, although the appearance, on the whole, is not so marked. The secondary pulvini display essentiallyt he same structure as the main pulvinus of the whole leaf, with the exception that the number of tannin cells is very

much greater.* When stained with chromic acid the protoplasm of the tannin cells exhibits a distinct appearance of reticulation, but from what cause I am at present ignorant.

Amicia zygomeris.—The pulvinus of this highly interesting plant was pointed out to me by Professor SACHS as well worthy of investigation. As a most striking example of both periodic and irritable movements this plant has apparently escaped general observation. It is particularly sensitive to alternations of day and night, and assumes the sleep position long before even such plants as *Robinia*. If violently shaken the leaves will, after a time, fall, and will be similarly affected some time after being cut and placed in water: the large size of the leaves rendering the least movement very conspicuous. Since it was the secondary pulvini that were especially movable, and they were, at the same time, of a comparatively large size, I used them in preference to still larger main pulvinus.

The chief characteristics of the pulvinus tissue of *Amicia* are the thinness of the walls of the parenchymatous cells, the extremely unlignified character of the vascular bundle and the remarkable development of a system of large pits, which is in this case extremely pronounced. The whole tissue is very succulent, and easily admits of thin sections being cut (Plate 68, fig. 9).

On treating with iodine and Chlor. Zinc Iod. the pits are, as usual, markedly brought into view. From the contrast of the deep blue coloration of the walls with that of the pits, it appears, at first sight, that no staining of the latter has taken place. Sections transverse to the pit, however, show that both a very slight staining of the pit-membrane has occurred, and that the membrane is extremely thin. In some of the pits small masses of protoplasm may be recognised sticking to the pit-membrane, being brought into view in consequence of their brown staining reaction. The pit-membrane is well stained by methylene blue. Scarcely any difference can be detected between the thickness of the cell-walls on the upper and under sides of the pulvinus. Except just beneath the epidermis, and next the vascular bundle, the cells are relatively large. The layer of protoplasm (primordial utricle) lining the cell-wall is thin, and the central vacuole is large. In consequence of this, very great shrinking of the protoplasm is possible, and experience shows that the successful preservation of this tissue is extremely difficult. Any reagents causing the least diffusion very soon affect the protoplasm, and the only at all successful treatment is brought about by

* The fact deserves notice that in the cases where the protoplasm displays any great activity of function, the cells of such a tissue usually contain tannin. For example, pulvini of *Mimosa Robinia*, *Desmodium*, &c., leaf of *Dionæa*, *Drosera*. Again in galls, where a stimulation of the protoplasm followed by rapid growth occurs. Notice that in *Robinia* it is the pulvini of the leaflets that move more than the main pulvinus, which have the greater quantity of tannin. The effect of tannin in producing aggregation is dealt with by A. F. W. SCHIMPER ('Bot. Zeit.,' 14, 1882) On Tannin. See also GARDINER "On the General Occurrence of Tannin in the Vegetable Cell, and a Possible View of its Physiological Significance." Proc. Camb. Phil. Soc., vol. iv., pt. vi., pp. 387–394, and Bot. Central. Bd. xvi., No. 48, p. 258.

means of saturated, watery, picric acid. Absolute alcohol is quite unsatisfactory. In the same way sulphuric acid causes very great contraction, the processes being usually ruptured, and nearly always pulled perceptibly from the pit membrane.

The cell-walls possess that peculiar semi-horny structure which is equally shared by so many of the Leguminosæ, and swell greatly with sulphuric acid. The delusive and at the same time very beautiful effects obtained by staining a section after treatment with sulphuric acid with methyl violet have already been dealt with under the head of pit membrane (Plate 68, fig. 10). As there mentioned, the bottom and sides of the pits are markedly stained by this reagent in a way somewhat similar to that of the protoplasm, and at first sight the appearance suggests that the cells are freely connected —the one with the other—by unbroken protoplasmic threads. The whole structure is remarkably like that of an enlarged representation of free cell formation. However, on treating the section with glycerine, all the deception disappears with the solution of the colouring matter, and it will then become apparent that in reality the connexion is neither so well defined nor so pronounced as in the case of *Mimosa* and *Robinia* (Plate 68, fig. 11). In no instance, so far as I can ascertain, do the processes approximate to one another in the unbroken way in which they appear to do in *Mimosa*. In the larger cells occupying the middle layer between the epidermis and vascular bundle, the protoplasm is either entirely pulled from the pit membrane, or the processes which at first connected the protoplasm of the pit with the general protoplasmic mass are ruptured so as to leave a short portion only sticking to the pit membrane. In the four last layers of cells which abut on to the vascular bundle where the cells are smaller with thicker walls and smaller vacuoles, it will be seen that although shrinking has taken place, yet the whole appearance of contraction is not so great although the protoplasm projecting into the pits has, as a rule, been pulled from the pit membrane. In the swollen pit membrane between the two symmetrically placed processes the same stained structure is apparent as occurs in the bast fibres of *Mimosa*, although the whole appearance is much more marked (Plate 68, fig. 11). The stained portion as before, and more markedly, suggests an appearance of striation, but with the strongest powers at my disposal, consistent with clear definition, I was unable to resolve the structure into fine threads. All that one can say is that its reactions point to its protoplasmic nature. In such of the other cells of the larger celled tissue as could be favourably observed, the same structure was present. It may here be mentioned that in cases, *e.g.*, *Phœnix* (Plate 69, fig. 13), where with a high power a sieve plate arrangement can be seen, and the threads clearly made out; with a low power the same appearances are produced as in the case in point, or as in bast fibres, and it seems probable that here a sieve plate arrangement does in reality occur.

The staining of that portion of the pit membrane which colours with aniline blue or which is left stained by methyl violet after prolonged action of glycerine, must not be confounded with the coloration of the bottom and sides of the pit which occurs with methyl violet alone or with methylene blue after the action of sulphuric acid. In

the latter instance the pit, as a whole, stains. In the former it is the staining of a substance other than pit membrane which runs through the latter, and which, by its different reactions, is to be separated from the pit membrane itself. Its reactions, as before-mentioned, point to a protoplasmic character.

Experiments were made with other pulvini and other organs of similar character, the results of which are detailed below. The experiments were somewhat hurried as the season was late, and although, to the best of my belief, the results are accurate, yet I do not regard them as perfectly conclusive, and I must work over the subject in detail on a future occasion.

Phaseolus multiflorus appears to be connected as *Amicia*.

Desmodium gyrans resembles *Mimosa* in structure.

Dionæa muscipula.—Sections of the tissue next the vascular bundle showed the cells to be connected as in *Mimosa*. In the epidermal and sub-epidermal layers this structure was especially evident, and some processes were seen uniting the glands with the cells.

Stamens of Cynara.—The lengthy oblong cells surrounding the central bundle appeared connected one to another principally through their end walls, in a manner almost exactly resembling that of a sieve tube. Apparently some connexion between them also took place through the side walls.

Tendrils.—In the oblong cells of the tendrils of *Bryonia*, a similar sieve-tube-like arrangement appeared to occur, especially on the end walls.

On the structure of endosperm cells.—From some points of view I could not regard the results I had obtained with pulvini as either perfectly satisfactory or perfectly conclusive. In spite of a probability little short of certainty, some doubt still remained; for it could be brought forward, that in the first place the results had been obtained by means of an extremely powerful reagent, with whose action we were by no means intimately acquainted; and, secondly, that we had no such examples of the general perforation of the pit-membrane by protoplasmic threads. And even allowing that the pit-membrane was traversed by fine threads, the great question that required answering was—Do these threads in reality cross the middle lamella, or is it only a case of the membrane itself being pitted, and the threads running up to the lamella, but no further?

In order, therefore, to put my results on as firm a basis as possible, it was necessary to experiment with my methods upon any such cases as might exist, where the passage of protoplasmic threads through the cell-wall was a confirmed fact, or to endeavour to establish, in a manner which admitted of no doubt, other instances of the existence of similar phenomena.

The first and most obvious examples of the occurrence of the perforation of the cell-wall are naturally afforded by sieve-tubes, and, in consequence, I began by investigating the results produced upon such structures by the reagents which I had employed in the case of pulvini.

In this direction I found that the method was in every way peculiarly adapted to show the intimate structure of sieve-tubes. In the course of my investigations on pulvini I had frequent opportunities for observing sieve-tubes, *e.g.*, in *Mimosa*, *Robinia*, &c. In both the above-named cases the sieve-tubes are very small, but treatment with sulphuric acid, and subsequent staining with methyl violet and glycerine, or HOFMANN'S blue, brought out these structures very successfully, and defined in an extremely clear manner the very fine threads connecting the contents of neighbouring tubes. The sieve-tubes of *Dahlia variabilis*, *Ricinus communis*, and *Phaseolus multiflorus* were also investigated. In *Ricinus* the youngest sieve-cells where perforation had not yet taken place were clearly demonstrated. In *Phaseolus* the general occurrence of a lenticular highly refractive body in the sieve-tube cavity was noticed, but I must defer a description of it until a future occasion.

But in the end the fact became apparent that although the results obtained with sieve-tubes gave very valuable proof of the success of the method I had adopted, yet that their structure could not be exactly compared to that of the parenchymatous cells of pulvini. Thus, in sieve-tubes, the cell-walls tend to assume a soft and somewhat mucilaginous character, and in them the middle lamella is but little developed, and the whole wall readily dissolves in sulphuric acid.

In the cells of the pulvinus, on the other hand, the walls greatly resist the action of the acid, and the development of the middle lamella is essentially pronounced.

There was, however, still one road left open, and that was to investigate the structure of thickened endosperm cells where all the requisite conditions were present, and what was of greater importance still, where the pit membrane was extremely thick, and would be likely to show plainly the existence of threads traversing its substance.

Some results had already been obtained in this direction, for TANGL,* in 1880, in his paper on "Open Communication between the Cells of Endosperms," had shown that in *Strychnos Nux-vomica*, *Phœnix dactylifera*, and *Areca oleracea*, a communication between the protoplasm of neighbouring cells was established by means of fine protosplasmic threads running through the cell-wall. In *Strychnos* the walls were thick and devoid of pits, and the presence of the threads was not confined to any particular portions of the cell-wall, but they occur over the whole area. In *Phœnix* and *Areca*, on the other hand, it was by means of pits that the connexion was brought about; the pit membrane being perforated in a manner very much resembling that which takes places in a sieve-tube.

TANGL'S results with *Strychnos* were fully confirmed by STRASBURGER,† but in the case of *Phœnix* and *Areca*, he states that he was unable to see the threads with the clearness conveyed by TANGL'S figure, and although he says that the pit membrane of *Phœnix* is demonstrably porous, yet the general tone of his statements

* *Loc. cit.* † *Loc. cit.*

give one the idea that he has not been fully able to satisfy himself as to the structure by direct successful observation.

I then resolved to repeat for myself TANGL's experiments, and also to investigate in as thorough a manner as possible the endosperm tissue of other species of Palms, and of other seeds of a similar nature. This work was carried on in the Jodrell Laboratory of the Royal Gardens, Kew, during the first three months of the present year.

Of the Order Palmæ I have examined the seeds of typical representatives of a great number of the genera, and I have, in addition, investigated the structure of the endosperm of members of the following Orders, viz.: Leguminosæ, Rubiaceæ, Myrsineæ, Cornaceæ, Loganiaceæ, Hydrophyllaceæ, Iridaceæ, Amaryllidaceæ, Dioscoriaceæ, Melanthaceæ, Liliaceæ, Smilaceæ, and Phytelephasieæ.

A mere glance at the foregoing list will be sufficient to show that a very large number of seeds were required, although from the great resources of the Royal Gardens I found no difficulty in obtaining typical representatives of any of the genera, and I cannot speak too highly of the great kindness I received on every side, from the Kew authorities, both in rendering me every assistance, and enabling me to obtain whatever material I was in need of for my investigation. Especially do I owe a debt of gratitude to W. T. THISELTON DYER, Esq., the Assistant Director, not only for the help I always received from him, but also for the kindly interest he took in my work all along.

Of the methods I employed I have already spoken in the earlier part of this paper. The usual plan I adopted was to cut with a razor, wetted with water, thin sections of the seeds, which were then stained with iodine and mounted in Chlor. Zinc Iod. Usually they could be examined at this stage; the exceptions being in those cases where the pit membrane rapidly assumed the blue cellulose coloration. After the prolonged action of Chlor. Zinc Iod. they were washed in water stained with picric-HOFMANN's-blue, and after a second washing in water were mounted permanently in glycerine (strong or dilute) or glycerine jelly.

In certain cases some slight modification of this process had to be resorted to, which was occasioned by the peculiar characteristics of the tissues in question. Thus, for example, in such endosperms as *Strychnos* or *Tamus*, where great swelling takes place upon treatment with water, the sections were cut in alcohol, stained with alcoholic iodine, and after treatment with Chlor. Zinc Iod. were washed with dilute alcohol; stained, and mounted in strong glycerine after having been well stirred in glycerine, on taking out of the staining fluid, instead of washing with water, although usually quick washing with water will succeed equally well. Again, where the pit membrane was thin, and taking up water soon became coloured blue with Chlor. Zinc. Iod., and would only for a short time retain its primary yellow coloration: such tissue was also stained with dilute alcoholic iodine.

The strength of the iodine must be altered as the nature of the material requires.

Thus *Phytelephas* or *Lodoicea* require a strong solution of iodine, while *Ruscus* or *Colchicum* will quickly assume a dark yellow with a solution of a comparatively weak strength. Treatment with sulphuric acid was also resorted to, not only as an alternative method, but also for the purpose of confirming my results with pulvini; although, from the very great thickness of the walls and the consequent enormous swelling which occurs, it was found that, as a rule, Chlor. Zinc Iod. was the preferable reagent for ordinary use.

On repeating the observations already made upon *Strychnos Nux-vomica* my results fully confirmed those of TANGL and STRASBURGER in every particular; and in thin and carefully-prepared sections it can be plainly seen that the threads do cross the middle lamella. Like TANGL, I was unable to stain the threads with reagents in the usual manner; and, in consequence, I instituted those experiments which led me to adopt that particular modification of dissolving HOFMANN'S blue in picric acid, and using it as a stain, which I have already dwelt upon in the earlier part of this paper. When by the use of alcohol the extreme swelling which takes place upon treatment with water is prevented, sections may be stained with picric-HOFMANN'S blue, and after mounting in strong glycerine may be successfully observed.

With regard to *Strychnos potatorum*, I am disposed to agree with STRASBURGER that a sieve-plate-arrangement does exist between the pits, for a striation could certainly be made out. However, the seeds I had to work upon were extremely old, and as such I look upon the results obtained with them as unsatisfactory.

As regards the structure of *Phœnix dactylifera*, when treated with iodine and Chlor. Zinc Iod. I came to the same conclusions as Professor STRASBURGER* that, although a striation could be observed, the threads were not nearly so clear as TANGL'S drawing represents, and, indeed, were made out with difficulty. After treatment with sulphuric acid, washing, and then iodine-staining, they were defined much more clearly; but the best and in every way most satisfactory results were obtained by staining the washed-out sections with HOFMANN'S violet and glycerine. In the latter case the stained protoplasm was contracted, and running through the pit membrane could be seen well-coloured threads presenting a distinct sieve-plate-arrangement (Plate 69, fig. 13).

In the same way *Areca oleracea*, usually known as *Euterpe oleracea*, at first gave a very feeble result when treated in the usual way; but, after a great number of trials and the use of strong iodine, and a prolonged action of Chlor. Zinc Iod., delicate threads could be plainly observed, which, moreover, appeared to cross the little developed middle lamella.

Having obtained the above-named results I commenced the examination of a number of palm seeds and of other seeds possessing a similar structure, in the hope of being in the end able to make some statements as to their general histology and to determine how far such a structure was of general occurrence. The following is the list of the palm seeds examined. I am indebted to Sir JOSEPH HOOKER for kindly

* *Loc. cit.*

looking over this list for me and not only making several valuable alterations, but also adding the authority for each species.

Arecineæ.
- Areca triandra. Roxb.
- Areca Catechu. L.
- Stevensonia grandifolia. Duncan.
- Rhopalostylis sapida. W. and D.
- Howea Belmoreana. Ben.
- Kentia costata. Ben.
- Archontophœnix Cunninghamii. W. and D.
- Euterpe oleracea. Mart.
- Euterpe edulis. Mart.
- Hyophorbe Verschaffeltii. Wendl.
- Synechanthus fibrosus. Wendl.
- Didymosperma distichum. H.f.
- Pinanga latisecta. Bl.
- Heterospathe elata. Scheff.
- Caryota urens. L.
- Manicaria saccifera. Gærtn.
- Cyrtostachys Renda. Bl.
- Calyptrogyne Swartzii. H.f.
- Calyptrocalyx spicatus. Bl.
- Chamædorea tinella. Wendl.
- Prestœa pubigera. H.f.
- Ceroxylon andicola. H. and B.
- Oncosperma horridum. Scem.

Lepidocaryeæ.
- Calamus calicarpus. Griff.
- Mauritia flexuosa. Linn f.
- Calamus fissus. Bl.
- Plectocomia Himalyana. Griff.
- Pirgafetta elata. Becc.
- Raphia Hookeri. M. and W.

Borasseæ.
- Latania Loddigesii. Mart.
- Lodoicea Sechellarum. Mart.
- Geonoma vaga. Griseb and Wendl.
- Bentinckia Conda-panna. Berry.

Coryphineæ.
- Thrinax, sp.
- Corypha elata. Roxb.
- Licuala Rumphii. Bl.
- Livistona Hoogendorpii. T. and B.
- Washingtonia filifera. Wendl.
- Sabal umbraculifera. Mart.
- Rhapidophyllum Hystrix. W. and D.

Cocoineæ.
- Cocos nucifera. L.
- Cocos flexuosa. Mart.
- Bactris, sp.
- Astrocaryum rostratum. H.f.
- Syagrus botryophora. Mart.
- Martinezia Aiphanes. Kl.
- Maximiliana caribœa. Gr. and W.
- Desmoncus, sp.
- Martinezia caryotifolia. H. and K.
- Guilelma speciosa. Mart.
- Diplothemium, sp.

Phytelephasieæ.
- Phytelephas macrocarpa. R. and P.

Phœniceæ.
- Phœnix dactylifera. L.

In all the above seeds a direct means of communication between the cells of the endosperm was observed.

Confining myself at first to the Palmæ, I would point out that in their structure the various seeds present every possible modification both of thickness or thinness of the pit membrane, of clearness or difficulty of observation, of variations in the size of the cell, and in degree of development of the middle lamella.

In making the subsequent observations with reference to the study of a number of instances of one and the same phenomenon, I propose to deal with the subject in a somewhat general manner and to illustrate my statements by such typical examples as will best serve my purpose.

I. *Development.*—In no case have I worked out the development of any of the seeds that I have examined. On account of want of time and opportunity, it is, there-

fore, a subject which must be reserved for another occasion. I would only draw attention here, to the striking similarity which the arrangement of the protoplasmic threads joining the cells of such endosperms as *Strychnos*, *Tamus*, or *Dioscorea* presents to the same arrangement of achromatin fibres which accompanies the development of the similar structure in *Agrimonia Eupatoria*,* and the close resemblance of the barrel form, so beautifully shown by *Heterospathe*, *Bentinckia*, or *Lodoicea*, to the like form assumed by the fibrillæ between the dividing nuclei in such endosperms as *Caltha palustris*,† or, indeed, in cell division in general. As TANGL‡ remarks, it seems as if the fibrillæ persisted during the subsequent cellulose formation and deposition. The appearance, perhaps, suggests that such is the case, and that the particles of cellulose have been deposited around the threads. It may also be noticed that no instance of a reticulate arrangement of the threads has been observed. In any case it is apparent, of course, that grave alterations must be occasioned by subsequent growth and increase in size of the cells, but anything certain development alone can decide.

II. *Structure of young endosperm cells.*—A number of observations were made upon the young endosperms of *Archontophœnix Cunninghamii*, *Sabal umbraculifera*, and *Rhopalostylis sapida*. In all these cases it was found that when the cell was still living, as could be seen from the presence of a well-developed nucleus, the connexion between the cells was fully maintained, and therefore that communication had existed in any case from a very early period (Plate 69, figs. 14 and 15).

As the cells grow older profound changes take place in the protoplasm, which usually result in the death of the cell. In order to ascertain the fate of the nucleus, portions of ripening seeds of *Archontophœnix elegans* and *Rhopalostylis sapida* were treated for twenty-four hours with saturated watery picric, and well washed with alcohol, until the yellow colour of the acid had quite disappeared. Sections were cut, which were stained with hæmatoxylin, and mounted in dilute glycerine. It was then apparent that well stained nuclei were present in the cells occupying the central portion of the seed (Plate 69, fig. 15), and as one gradually traced the staining effects from within, outwards, it was seen that the nearer the periphery, the less conspicuous became the cell-nucleus, until in the outermost layers no trace of a nucleus could be detected; its substance staining less and less, and its outline becoming more and more badly defined. Thus it apparently suffers a complete disorganisation.

Along with changes of the nucleus proceed alteration of the protoplasm. In many seeds—*e.g.*, *Phytelephas*—but little protoplasmic substance appears to remain in the cell. Oil very frequently occurs as a cell content, and sometimes is present in large quantities, especially in the Cocoineæ—*e.g.*, *Cocos*, *Bactris*, &c. Small crystals may also occur, and in such examples as *Diplothemium*, *Syagrus*, and *Corypha* aleurone grains are met with. In the cases which I examined with special reference to the

* STRASBURGER, 'Zellbildung und Zelltheilung,' Tafel I., fig. 15. † *Loc. cit.*, Tafel II., fig. 31.
‡ *Loc. cit.*

question the cells appeared to be quite dead, and as such they are simply preyed upon by the growing embryo. Thus, all the changes which result in their subsequent breaking down proceed from the embryo itself.

Special experiments were made with sulphuric acid, in order to observe its action in cases where a continuity was known to exist. In fresh living cells treatment with sulphuric acid, and staining with methyl violet and glycerine or HOFMANN'S blue, showed that, although the protoplasm had contracted, those portions projecting into the pits still adhered to the pit membrane, and that the threads of protoplasm running through the pit membrane were continuous on either side with the above-mentioned symmetrically opposite processes (figs. 14 and 15). The processes, in fact, appear to be held to the pit membrane by the threads in question in all cases where the continuity is pronounced. Under a low power the individual threads could not be distinguished, and the appearance then presented was that of two darkly-stained threads united by a lighter-stained area running between them—in fact, the very appearance presented by *Mimosa* and *Robinia** (*cf.* figs. 5, 7, 14, and 15). In the case of ripening seeds, the protoplasm may be made to contract slightly from the membrane, and then a similar phenomenon is induced to that which occurs in *Amicia* and the bast cells of *Mimosa* (*cf.* figs. 11 and 13), although in them it is not occasioned by loss of vitality, but rather from the fact that the threads are probably extremely fine and the continuity not so pronounced as it is in the case of the parenchyma cells. In fully-ripe seeds where the cells are dead, the protoplasm always contracts away from the cell-wall, and a similar state of things usually occurs when the cell has been killed by the action of reagents (see figs. 16 and 22). Thus, both my method and my results have received very satisfactory confirmation and elucidation.

III. *General results with ripe endosperms.*—As a rule, most of the seeds I examined were either one or, at most, two years old. I also made use of some museum specimens, but decided to reject the results I obtained with them, as I had reason to believe that in many cases those results were abnormal. As regards their favourable or unfavourable character as material for showing the perforation of the cell-wall by protoplasmic threads, seeds greatly differ one from another. In the first place, it may be stated, as a general rule, that the thicker the pit membrane the easier can the threads be distinguished. In very thin pit membranes the observation of such threads as may cross it requires great precaution and care; there is nothing, so to speak, for the eye to catch upon, and one has to detect a line within a line. It is this very fact that causes endosperm tissue to be so favourable for such an investigation as the present one; for here, not only, as a rule, are both the cells and the pits unusually large, but, what is much more important, the pit membranes are thick. In many cases, however, this is not the case, and an examination of such examples as *Manicaria*, *Mauritia*, or *Caryota* is quite sufficient to prove that the

* The results with *Bomarea* also confirm this.

successful observation of the threads crossing a thin pit membrane is a matter of extreme difficulty; and it also serves to show that in other cases where the pits are very small and the membranes very thin this difficulty is so increased as to become almost an impossibility.

But apart from any consideration of the pit membrane, the ease or difficulty of observation also appears to depend greatly upon the peculiar characteristics of the seed itself. For instance, as I stated at the outset, *Phœnix dactylifera* and *Euterpe oleracea* are inclined to be unfavourable material. In *Euterpe edulis*, on the other hand, the connecting threads can be easily demonstrated. Of numerous other instances, *Geonoma*, *Plectocomia*, *Areca triandra*, *Areca catechu*, and *Cocos nucifera*, afford examples of cases where difficulties of observation occur.

Among the most favourable material for examination are the endosperms of *Bentinckia*, *Stevensonia*, *Thrinax*, *Heterospathe*, *Syagrus*, *Corypha*, *Howea*, and *Lodoicea* (see figs. 16, 17, 18, 22, and 25). The degree of development of the middle lamella varies greatly. As a rule, in thickened endosperms it attains but little development, or, even if this be not the case, it stains but little, and its refractive index varies only slightly from that of the general cell-wall. In *Calamus*, *Sabal*, *Raphia*, and *Ptychosperma*, the lamella is decidedly pronounced. In such cases as *Stevensonia* and *Calamus* (Plate 69, fig. 24) both the middle lamella and the threads are well developed; and though in them there is some difficulty in determining whether the middle lamella is actually perforated by the protoplasmic threads, yet, as a rule, careful examination and preparation will decide that in the vast majority of cases it can be seen that such perforation does occur, and such examples as *Heterospathe*, *Kentia*, *Mauritia*, or *Bentinckia* do away with all possible doubt (figs. 16, 19, 22, 23). As to the manner in which the communication between the endosperm cells is established, experiment shows that there are two possible ways which essentially depend upon the configuration of the cell.

In such exceptional cases as *Strychnos*, *Tamus* (Plate 70, fig. 33), and *Dioscorea*, where the walls are extremely thick, and, at the same time, devoid of pits, the communicating protoplasmic threads run through the cell-wall. A section of such an endosperm exhibits the threads, which are seen freely perforating the wall, except at the corners of the cell, at the point where the junction of several cells occurs.

The usual mode of union, however, is by means of pits. As I have mentioned elsewhere, the presence of pits in the cell-wall, due to unequal thickening, is of almost universal occurrence, and it is through the closing membranes of such pits that the protoplasmic threads run. This, in fact, appears to be by far the most common and typical way in which the continuity of the protoplasm of adjacent cells is brought about.

In other, and perhaps less frequent cases, examples of both modes of connexion occur; the communication taking place not only through the pits, but through the

walls as well. I have observed that this happens in *Kentia Belmoriana*, *Kentia costata*, *Lodoicea*, *Bentinckia*, and *Asperula* (see figs. 16, 17, 19, 31); but I am led to believe that such union is of much more general occurrence. In all the foregoing examples, the threads running through the walls are more especially obvious in the cells just below the surface, and gradually become less and less visible, as one approaches the central tissue of the seed. This appears to me to be simply an arrangement for insuring that every facility should be given for the passage of nutritive material from without inwards, and also that it should have opened to it as many channels as possible. It is obvious, for instance, that the amount of plastic formative substance required for building up such a tremendous endosperm as that of *Lodoicea* must be very considerable, and even supposing its growth to be slow, the drain on the nutritive material must be large, and the rate of its flow must be very great. Consequently the increased facilities for easy transmission must be of great advantage. And not only in the development of the endosperm, but also upon germination, is this structure of great use to the plant, for at that period the outer cell-layers will have become very dry, and consequently the difficulty of their being broken down by the absorbent foot of the cotyledon will be increased. But at the same time, owing to the greater development of a system of channels in them, they are more easily permeated and wetted by the cell sap holding in solution the ferment which will bring about their final disorganisation.

The form presented by the aggregate of threads traversing the pit membrane is usually that of the well-known basket or barrel-shape which is met with in connexion with nuclear division. In many instances, and especially in *Bentinckia*, the shapely sweep of the curving threads, and the graceful arrangement of the whole thread-complex is extremely striking and beautiful (Plate 69, fig. 16). In other cases the bending of the curve is not so marked, and in very thin pit membranes—*e.g.*, *Synechanthus*, *Livistona*, &c.—the threads appear to be altogether straight.

In the instances where the threads go through the cell-wall their direction is seldom straight, but usually bent, and resembling in arrangement the appearance presented by the achromatic fibres during free-cell-formation.

Every variation occurs both as regards the size of the cells, the distribution of the pits, and the number and thickness of the threads. Thus, whereas the cells of *Caryota urens* and *Lodoicea* (Plate 69, fig. 19) are large, those of *Thrinax* and *Geonoma* are small. In such endosperms as *Manicarea* and *Chamædorea* the pits are very numerous, while in *Washingtona* but few are present. In *Calyptronoma* the threads are few and somewhat stout, while in *Oncosperma* they are very numerous and fine. In *Bentinckia* and *Heterospathe* they are also many in number. The threads are made very conspicuous by staining with iodine and treatment with Chlor. Zinc Iod., for the latter reagent appears to cause a decided precipitation of iodine upon them as well as upon the general protoplasm which is accompanied by an increase in

apparent diameter. That this is actually the case may be demonstrated either by reversing the operation and staining with iodine after treatment with Chlor. Zinc Iod. and subsequent washing, or by staining with picric-HOFMANN'S-blue. (Compare Plate 69, figs. 22 and 23.)

As a rule nothing can be seen of the threads when a section of endosperm tissue is mounted and stained in the usual manner. But to this statement *Bentinckia* affords an exception, for here an appearance of striation can be detected, and in *Stevensonia* staining with HOFMANN'S violet alone makes the threads apparent. Treatment with iodine, picric acid, or with a mixture of iodine and glycerine will also often bring them into view, *e.g.*—*Lodoicea* (Plate 69, fig. 20), *Latania*, and *Bentinckia*.

Experiments with the object of injecting the threads with colouring solutions met with no success. Pieces of the endosperms of *Latania* and *Calamus* were fitted into a bored india-rubber cork, which was then tightly fastened into one end of a manometer tube, the shorter arm of which contained the solution of the colouring matter, and the longer held the mercury by means of which the injection-pressure was induced. First, a solution of water-blue in water was employed, and as this caused swelling of the wall a solution of insoluble blue in alcohol was used in preference. However, when exposed to the pressure of a column of mercury of sixty inches no injection occurred.

Besides the particular methods I have chosen for the elucidation of this subject, many others were tried with little or no success. Sections of *Bentinckia*, as being favourable material, were treated in the usual way with solutions of gold chloride and silver nitrate, but with no result. In every case it was found that it was necessary to swell the cell-wall before staining. After swelling with Chlor. Zinc Iod. and washing, silver nitrate was again tried, and this time with some small amount of success. I adopted a modification of treating the section with sulphuretted hydrogen-water, after exposure in a 2 per cent. solution of silver nitrate for half-an-hour, and subsequent washing, instead of reducing the silver by the action of light, as in the usual process. The result was perhaps better, but still far from satisfactory, and would be quite inapplicable in any case where the threads were not particularly well developed. Some sections, after swelling, were treated with an alcoholic solution of tannin, and when washed were shaken up with a solution of ferric chloride. The wall then coloured the usual blue-black, and the colourless threads could be seen fairly well. Other sections, again, were soaked in a solution of ferric chloride, and after washing were treated with a solution of potassium ferrocyanide. In this case the threads were less clearly defined than with tannin and iron. Lastly, sections were treated for some time with a solution of corrosive sublimate, in the hope that an insoluble compound might be formed with the remains of the cell protoplasm. After washing the section was shaken up in sulphuretted hydrogen-water, but with no good result. Thus all these experiments pointed to the fact that my methods, if not perfectly satisfactory, were at least fairly successful.

In concluding the subject of Palm endosperms I might make a few remarks upon some particular examples which appear to be of equal interest.

In all the seeds nearly related to *Calamus* the structure is very typical (Plate 69, fig. 24). I have already noticed the great development of the middle lamella in these endosperms. Another interesting fact is, that in *Calamus* and *Metroxylon* a well-marked cubical crystal is present, imbedded in the wall of each cell. It seems as if there had been a period in the life of the cell when the protoplasm had required to get rid of some of the calcium oxalate resulting from the metabolic activity of the protoplasm. This was consequently thrown down in the form of a crystal which adhered to the cell wall, and in the subsequent thickening which occurred, was gradually covered in until it was at length surrounded on all sides by the cellulose.

Lodoicea sechellarum is of interest, not only as affording one of the clearest examples of the perforation both of the wall and pit membrane, but also because of its very unique distribution (Plate 69, fig. 19).

In *Oncosperma* the threads are excessively fine, and certainly suggest the extreme probability of the existence of threads which are so delicate as to be invisible (Plate 69, fig. 21). In fact, I am inclined to believe that this really is so in such endosperms as *Cocos nucifera*. To this seed *Martinezia caryctifolia* presents a useful transition. With iodine it can be seen that very fine threads do go through the almost smooth walls, but upon treatment with picric-HOFMANN'S-blue the individual threads cannot be distinguished, and only a blue coloration occurs. In *Cocos*, which has essentially the same structure, I was unable to observe threads, though I cannot doubt that such threads do exist. In all the *Cocoineæ* the walls are thin and must be carefully examined. They are, however, of extreme value, both from the point of view of analogy and comparison. In *Syagrus* (Plate 69, fig. 25) and *Desmoncus* the threads are well seen. *Heterospathe elata* is a particularly favourable endosperm for demonstrating the perforation of the middle lamella, which here is but little developed (Plate 69, figs. 22 and 23). The threads appear very clearly with iodine. In *Phytelephas*, although the walls are extremely thick the pits are small, the pit membrane somewhat thin, and the threads are demonstrated with difficulty. The cells contain but little remains of the protoplasm, and several results have induced me to think that the amount of solid matter in the perforating thread channels is so small that the channels are practically empty (Plate 70, fig. 26).

These results seem to show that in all the Palmæ the structure of the endosperm cells is similar.

Endosperms other than those of Palms.—As I have remarked elsewhere, the endosperm of Palm seeds is particularly favourable material for an investigation of the perforation of the cell wall by protoplasmic filaments. And, speaking generally, in the examination of most endosperms other than those of the Palmæ, additional difficulties are presented which greatly interfere with successful observation. Especially does it become apparent that the thickness of the pit membrane is not

nearly so great, and this fact both increases the difficulties of making out the threads, and in consequence of the rapid blue coloration of such a thin membrane causes the observations with iodine and Chlor. Zinc Iod. frequently to be almost valueless and often an impossibility. It is in such cases that my staining method comes to be so important.

Often it would seem that the threads are so excessively fine that they cannot be resolved as separate filaments, and the appearance presented by the whole aggregate of threads crossing the pit membrane is simply that of a blue coloration. In this direction the results with *Bomarea* are of special interest, as they tend to give weight to the view that my experiments have led me to adopt, viz.: that a well defined blue coloration, after the action of Chlor. Zinc Iod. and picric-HOFMANN's-blue, points to the presence of protoplasmic threads in the cell-wall.

Professor STRASBURGER * states, in the case of the endosperm cells of *Ornithogalum* and in the pith cells of *Taxodium*, that the pit membranes are demonstrably porous, and that a striation can be observed crossing the membrane upon action with iodine and Chlor. Zinc Iod. He also represents this striation in figs. 17, 18, 19, and 23, Tafel I.; and again in fig. 23, Tafel II., he shows that a similar striation may be seen in the closing membrane of the pits in the thickened cells of the seed-coat of *Viscum*.

As far as regards *Ornithogalum* I can fully confirm his results, and the fact of the existence of a similar structure in *Taxodium* and *Viscum* is one of great value.

Staining with picric-HOFMANN's-blue, subsequent to the action of iodine and Chlor. Zinc Iod., will demonstrate in the case of *Ornithogalum* that the pit membrane is distinctly blue, while the rest of the cell-wall is practically colourless, and will also bring out more clearly the striation of the pit membrane, due to the presence of threads. This, however, is by no means a favourable case.

Sections of the endosperm cells of *Bomarea oligantha*, after swelling and staining, gave me good results. If examined in a somewhat cursory manner it is at once observed that the pit membrane is well coloured and distinctly delineated from the rest of the cell-wall (Plate 70, fig. 27). In some instances it can be observed that instead of the whole pit membrane being uniformly coloured, it may be traversed by one or two coloured bands which run through the otherwise colourless substance of the membrane (refer to figure). In favourable instances well defined striation can be seen. In an *en face* view of the pits it becomes evident that the pit membrane exhibits essentially the same appearance as that presented by a sieve-plate (Plate 70, fig. 28), and the appearance of the two coloured bands is explained from the fact that in some instances the whole membrane is not necessarily perforated, but that the perforation and hence the sieve-plate structure may be confined to particular areas of the membrane of the pit. This particular distribution of perforating areas also explained the appearance of bifurcation, which is sometimes presented by the apex of much contracted protoplasmic

* 'Bau und Wachsthum,' p. 16, *et seq.*

processes when pulled out of the pit cavity in consequence of the action of strong sulphuric acid, or other dehydrating agents.

The staining results with *Bomarea* appear to me to give great support to the idea that a pronounced coloration of the pit membrane by picric-HOFMANN's-blue after the action of iodine and Chlor. Zinc Iod. gives evidence of the presence of protoplasmic threads in the cell wall and therefore of perforation.

In *Ruscus*, although the cells are large, the pit membranes are very thin and quickly coloured with iodine and Chlor. Zinc Iod. After staining in the usual manner fairly well defined threads can be seen (Plate 70, fig. 29). The same is the case with *Iris* and *Xiphium*.

Colchicum is a particularly plain example of perforation of the pit membranes, which are here somewhat thick. Both with iodine and with HOFMANN's blue the individual threads are easily distinguished (Plate 70, fig. 30). Of Dicotyledons exhibiting a similar structure, *Ardisia polycephala* is an example of some interest on account of its peculiar reaction with iodine. With a dilute solution of this reagent the substance of the cell-walls give a blue reaction, exactly resembling that of starch. Stronger solutions rapidly cause a dark brown coloration. The seeds of *Ardisia crenulata* behave in the same way. The same has been observed in the seed of *Pæonia*, and has been long known in the case of the phlœm of *Lycopodium*; the so-called fungus cellulose; and (when the iodine solution is of a certain strength) in mucilage cells. In *Nemophila*, although the cells are small, an appearance of striation is plainly evident (Plate 70, fig. 32). The structure of the horny seeds of certain of the *Rubiaceæ*, *e.g.*, *Coffea*, *Galium*, and *Asperula* (Plate 70, fig. 31) is of some interest. The cell-walls present a somewhat crumpled appearance, and there is no definite arrangement in their shape. After treatment with strong iodine and a lengthy action of Chlor. Zinc Iod., a system of fine threads is clearly brought into view. Where the wall is pitted, the threads go through the pits, or, if not, through the thick wall, as the case may be. This was observed in *Asperula* only. The rest were not examined in detail.

The structure of the seeds of *Tamus* and *Dioscorea* are very important as affording additional confirmation of TANGL's results with *Strychnos*. The thick walls of these seeds present no pits, and are of the same transparent horny nature as those of *Strychnos Ignatia*. After treatment with iodine and Chlor. Zinc Iod. the very numerous threads which freely perforate the entire thickness of the cell-wall gradually come into view, and resemble in both arrangement and properties those of *Strychnos*. The fact that the threads cross the middle lamella is even better demonstrated in *Tamus* than in the former instance, for here the development of the lamella is not so great. The cell-walls soon swell very strongly, and in so doing the threads are broken up into a number of points, as TANGL has observed, and in the swollen portion of the wall at last become invisible (Plate 70, fig. 33). In *Dioscorea* the threads are much finer than in either *Strychnos* or *Tamus*. In both instances threads can be observed uniting all

the cells, including of course those directly below the surface. In this respect they differ from *Strychnos* as far as their demonstrable character goes.

In such of the *Cæsalpinia* as possess endosperms a similar pitted structure of the cells occurs. The existence of threads was observed only in *Bauhinia*, but I cannot doubt that other leguminous seeds of the same structure will show the same occurrence of threads, *e.g.*, *Sophora Japonica* and *Gleditchia* mentioned by Von Mohl.*

Subjoined is a list of the seeds examined. In those whose names are printed in italics it was actually observed that there was a protoplasmic continuity from cell to cell. The rest were not examined in detail.

Leguminosæ.
Bauhinia variegata.
Rubiaceæ.
Asperula odorata.
Galium aparine.
Galium spurium.
Coffea Arabica.
Sherardia arvensis.
Myrsineæ.
Ardisia crenulata.
Ardisia polycephala.
Cornaceæ.
Aucuba Japonica.
Loganiaceæ.
Strychnos Nux-vomica.
Strychnos Ignatia.
Strychnos potatorum (?)
Hydrophyllaceæ.
Nemophila discoidalis.
Nemophila parviflora.
Phacelia pimpernelloides.
Melanthaceæ.
Colchicum speciosum.
Liliaceæ.
Asparagus officinalis.
Asparagus sp.
Ornithogalum tenuifolium.
Ornithogalum narbonense.
Yucca, sp.
Smilaceæ.
Polygonatum Japonicum.
Ruscus aculeatus.
Iridaceæ.
Iris pseudacorus.
Xiphium vulgare.
Iris ochroleuca.
Dioscoreaceæ.
Dioscorea dæmonorum.
Tamus communis.
Amaryllidaceæ.
Bomarea oligantha.

The above results have established not only that protoplasmic threads do perforate the cell-wall, and thus bring adjacent cells into communication with one another, but that such perforation is of very frequent occurrence. My results with endosperm cells have fully confirmed those which I obtained with pulvini, and have both elucidated the structure that occurs in those organs, and given every support to the methods that I employed in their investigation. It would thus appear that not only in the endosperms of Palms, but in those of other plants in general, the cells are placed in connexion one with the other. It may be objected that I have used thick walled endosperms in every instance. I gave my reasons for so doing, and although I have not as yet examined the structure of thin walled endosperm cells, I have but little doubt that the same means of communication takes place in them also, for every range of difference of thickness of the cell-walls occurs, not only in the same order but

* Von Mohl, 'Vegetable Cell,' English translation, p. 33.

in families of that order, that differ but little one from another. Russow's results are also of especial value here.

Results with Plasmolysis.—At an early stage in this investigation certain phenomena in connexion with experiments upon the preservation of tissues forced themselves upon my notice. What was especially striking was the different result which was obtained when different tissues were treated with the same reagent, and under the same conditions.

Thus, upon examination of sections of the pulvini of *Mimosa*, *Robinia*, and *Amicia*, which had been all carefully preserved in absolute alcohol, it will be seen that the degree with which the protoplasm is contracted from the cell-wall varies greatly in the three cases. In the cells of *Mimosa* the protoplasm will have undergone but little contraction, and the whole tissue will show signs of successful preservation. In *Robinia*, on the other hand, an appreciable contraction has evidently taken place, and in *Amicia* this state of things has attained a maximum, for almost every cell exhibits the much shrunken protoplasm lying freely in the cell cavity, and separated on all sides from the cell-wall. Since in every instance the cells are full grown, and are under equal conditions, it would seem probable that the protoplasm is held closer to the cell-wall in some cases than in others.

After having obtained my results with *Mimosa*, *Robinia*, and *Amicia*, it seemed the more probable that the above appearances were in reality a consequence of the intimate union between the cell-wall and protoplasm which my investigations had shown to exist, and the pronouncedness of which appeared to vary.

In consequence of these and other considerations, I was led to study, in a detailed manner, the effect of plasmolysing such cells, since it seemed to be almost certain that the phenomena accompanying such a condition would afford additional confirmation of the results I had already obtained with somewhat powerful reagents.* According to De Vries† when the plasmolytic condition is induced in a cell by means of dilute dehydrating agents, the protoplasm (primordial utricle) separates entirely from the cell-wall, and appears as a much contracted vesicle lying freely in the cell cavity.

On the other hand, both Pringsheim‡ and Nägeli§ had noticed that in certain cases the protoplasm appears to separate with some difficulty from the cell-wall, and that it was frequently connected to it by means of one or more threads in those cases where great contraction had taken place.

It had also been long known that in filamentous *Algæ*,‖ the protoplasm upon contraction is often connected to the cell-wall by threads. These, however, may be rather described as isolated cases, for no generalisations were made, nor was any

* Proc. Roy. Soc., Nov. 11, 1882.

† 'Untersuchungen über die Mechanischen Ursachen der Zellstreckung.' Leipsic, 1877.

‡ 'Bau und Bildung der Pflanzenzelle.' 1854.

§ 'Pflanzenphysiologishe Untersuch.' 1855.

‖ Hofmeister, 'Die Pflanzenzelle.' 1867.

particular attention drawn to the fact; on the contrary, it has been generally accepted that on plasmolysis the protoplasm is quite free from the cell-wall.

However, in repeating these experiments I find that in all the cases I have examined the contracted protoplasm is always connected to the cell-wall by means of very numerous protoplasmic threads.

The above phenomena were also discovered subsequently and independently by Bower,* whose excellent paper on the subject appeared shortly after my own. My experiments were first made upon pulvini, but were afterwards extended to tissues in general (figs. 34, 35, 36, 37).

The most detailed observations were made upon transverse sections of the pulvini of *Amicia zygomeris* and *Robinia pseudacacia*, after treatment with 2·5 per cent., 5 per cent., and 10 per cent. solution of sodium chloride, but since the results obtained in other cases differ so little, one may describe the phenomena which accompany plasmolysis in general terms.

If a dilute solution of salt be employed, *e.g.*, 2·5 per cent., the protoplasm will gradually contract away from the cell-wall, and will at length frequently appear to lie quite freely in the cavity. In other cases the protoplasm will adhere to the cell-wall at certain points. But if the section be examined for some time, it will be seen that delicate strings of protoplasm will gradually come into view, and increase in number, until at length the contracted protoplasmic mass will present the appearance of a sphere suspended in the cell cavity by innumerable fine protoplasmic strings (Plate 70, fig. 37).

If contraction be rapidly brought about by means of a stronger solution, *e.g.*, 10 per cent., it will be observed that the protoplasm experiences some difficulty in separating from the cell-wall, and may even become divided up during the process into two or more portions (Plate 70, fig. 35), each of which rapidly assumes a spheroidal shape; also several somewhat thick threads may be seen connecting the protoplasm to the cell-wall or the protoplasmic masses to one another (figs. 35 and 36). Subsequently the finer threads come into view. I am inclined to believe that it is these thicker threads which have been hitherto seen, and that the finer threads have, up till now, escaped observation; and although, as Bower† remarks, the difference between the thicker and the finer threads is only one of degree, yet the importance of the observation is in no way diminished thereby.

The thicker threads frequently present nodal swellings of a perfectly spherical form. These spherical nodes may either abut on to the cell-wall or may occupy any other position upon the thread. When, by chance, rupture of the threads occurs, part contracts to the central protoplasmic mass, and part forms a small sphere on the side of the cell-wall.

The first indication of the existence of the fine threads is afforded by an appearance

* Quart. Jour. Micr. Sci. Jan. 1883.

† *Loc. cit.*

of striation, which gradually becomes more and more defined until distinct threads can be observed. At first the diameter of the threads gradually diminishes from the protoplasm to the cell-wall, so that it is impossible to trace the thread over the whole of its course (Plate 70, fig. 40); but after some time it comes more clearly into view, until at length it is apparent that it extends right up to the wall in question.

The thickness of the threads varies greatly. Up to a certain point, more and more threads come into view the longer the cell is observed, until at length the appearance presented will be that of a central contracted sphere of protoplasm from which radiate out to the cell-wall numerous fine threads, some of which are of an appreciable size, other smaller though still well defined, and others so difficult to see that their presence is only indicated by a faint striation traversing the space between the protoplasm and the cell-wall.

The phenomenon of the gradual definition of the threads appears to suggest that a thickening of their substance has taken place, and as Bower* has observed, this in reality does occur.

He has seen also that the nodal swellings appear to travel from the protoplasm to the cell-wall, and is of opinion that the thickening of the threads is due in a great measure to a drawing out of fresh substance from the main protoplasmic body. He also suggests that lateral coalescence of the strings may occur. My view of the case, however, differs from his. It is certain that at first the protoplasm quickly contracts, owing to the rapid diffusion which occurs. The water diffuses from the cell vacuole into the salt-solution, much more quickly than the salt-solution diffuses into the water, so that the contraction of the protoplasm reaches its maximum when it has lost the greatest amount of water. After a time osmosis ceases, but not until the strength of the fluid, both inside and outside of the protoplasm, is the same. And in the subsequent equilibrium which occurs, the protoplasm, which had before suffered an abnormal contraction, owing to the rapid loss of the water it had contained; now takes up in exchange a small quantity of the salt-solution, and the ultra shrinking (so to speak) is relieved,† and a definite swelling of the protoplasm takes place. Thus the tension on the threads is no longer so great, and, owing to their elastic character, they thicken up and are thus brought into view. Subsequently they cease to thicken, and by the time the shrunken protoplasm has regained its equilibrium they become quite lax. Both Bower and myself have observed that, after some length of time has elapsed, the threads execute lateral vibrations which are possibly caused by currents due either to diffusion or to temperature.

It seems probable that the action of the salt-solution, unless very dilute, causes grave changes to take place in the protoplasm. Ordinary cells do not give much evidence of this, since on washing out with water they regain their usual appearance.

* *Loc. cit.*

† It loses, in fact (if I may be allowed to use the expression), some of its water of constitution, and takes up in its stead the salt-solution.

If, however, *Spirogyra* cells be plasmolysed, it will be seen that the whole structure has been much affected, for the chlorophyll bands will no more resume either their accustomed appearance or arrangement, and a general swelling of the cell takes place.

The strings of protoplasm which normally traverse the cell vacuole in ordinary living cells frequently exhibit the same appearances as those which are presented by plasmolysed threads, and nodal swellings may also occur. I have observed this particularly well in the hypodermal cells of potato tubers.*

I have also frequently noticed that as a result of plasmolysis many chlorophyll grains will tend to aggregate around the nucleus as if some connexion with the latter existed, such as PRINGSHEIM observed in *Spirogyra*.†

The point of special interest to me was to ascertain whether these threads bore any relation to the pits. As I stated in my paper before the Royal Society, I have observed several well defined instances in which threads do go to pits, and in Plate 70, fig. 34, which is a made-up figure embodying in one representation the results of numerous individual cases, I have attempted to illustrate such appearances. In one instance, where plasmolysis had been quickly induced by means of a strong salt solution, two spheres of protoplasm occupied the two opposite pit depressions, from each of which a thread ran to the main protoplasmic mass. However, numerous experiments have convinced me that no reliance can be placed upon the results obtained by plasmolysis, as giving any certain clue to the existence of protoplasmic continuity. With this opinion BOWER also agrees.‡ In fact, the greater proportion of threads bear no relation to pits, and in such an experiment as plasmolysing a hair of *Primula sinensis*, it is seen that as many threads go to the longitudinal as to the transverse walls, and are thus present on the free walls, as well as those separating contiguous cells (see also Plate 70, fig. 39).

As I mentioned in the earlier part of my paper, my efforts to fix and stain these plasmolytic figures did not meet with perfect success, although picric acid gave very satisfactory results. I am, however, inclined to think that additional shrinking was produced by the use of glycerine, and the method deserves another trial. As a result of the staining, both the threads and the protoplasm were well brought into view, but a very great proportion of the threads were ruptured, and appeared as little spheres attached to the cell-wall. I was unable to trace the protoplasm into the cell-wall, but at that time I had not adopted my plan of staining with picric-HOFMANN'S-blue. It is possible that with this reagent some results may be obtained. In my paper before the Royal Society,§ I stated that I had succeeded in showing the passage of the protoplasm through the cell-wall when the wall was left intact, and not swollen by reagents; the method consisting in treating thin sections of fresh material with saturated picric

* See figure of cell of hair of *Cucurbita*. SACHS' 'Vorlesungen,' p. 752.

† PRINGSHEIM, 'Über Lichtwirkung und Chlorophyllfunction.' Leipsic, 1881. Tafel XIV., fig. 4.

‡ *Loc. cit.*

§ *Loc. cit.*

acid. There are two mistakes in that statement. First I should have said "treating plasmolysed sections:" and what is of more importance, I am inclined to believe that my observations were not perfectly trustworthy. I had two particularly plain instances of an apparent passage of protoplasm through the cell-wall, one of which I have represented in Plate 70, fig. 38. Although it still seems perfectly clear and plain, I am almost convinced that some abnormal appearance has been produced, either by distortion of the section, or owing to the fact that, intersecting the two coloured protoplasmic threads, are thin pit membranes which I cannot resolve.

As regards plasmolysis, numerous tissues were examined, and in all the same occurrence of strings was observed. Both Bower and myself believe that the phenomenon is universal. As definite instances where actual observations were made I may mention the pulvini of *Mimosa*, *Phaseolus*, *Rhynasia*, *Oxalis*, *Biophytum*, *Apios*, *Desmodium*, *Maranta* and *Marattia*; various roots, *e.g.*, *Beta*; petioles, *e.g.*, *Primula* and *Ficus*; leaves, *e.g.*, *Primula*; young endosperm cells, *e.g.*, *Rhopalostylis*, *Sabal*, and *Aucuba*. Stems and other structures examined from time to time gave the same results. These results, taken in conjunction with those of Bower, make it extremely probable that the same phenomenon is displayed by every living cell whatsoever.

In attempting to explain these appearances which accompany plasmolysis one has only hypothesis to offer. Bower* suggests two views—(1) that the main mass of protoplasm on retreating may leave the cell-wall still completely lined with a thin film of protoplasm; (2) that the peripheral part of the protoplasm being entangled as a network among the deposited microsomata may, on the contraction of the main mass, be drawn out at the points of entanglement into fine strings like those observed; while the surface of the wall is left free, and not covered by a film of protoplasm.

But it seems to me that all the above phenomena may be explained from the mere fact that the cell-wall is so perfectly wetted (to use a physical phrase) by the protoplasm; for as Strasburger's† results show, the connexion between the cell-wall and the protoplasm is one of the most intimate description, even if any direct perforation of the cell-wall by protoplasmic filaments be left out of the question. The very same effects may be obtained with stringy mucus adhering to a glass tumbler. My results have certainly shown that the connexion between protoplasm and cell-wall is much closer than was imagined to be the case; but I am inclined to doubt whether the existence of protoplasmic threads in the cell-wall at all influences the phenomenon of plasmolysis, for they are equally well displayed over the whole surface of the wall, and bear no relation even to such pits as those occurring in the young endosperm cells of *Archontophœnix* and *Rhopalostylis*, where well pronounced continuity is known to occur. But I am bound to admit that it is a question of hypothesis against hypothesis, and I look forward with interest to the results of

* *Loc. cit.*

† 'Bau und Wachstum,' p. 246.

plasmolysing such a cell as *Tamus communis* (Plate 70, fig. 33). In concluding the subject I should like to state my views as to the reason why plasmolysis does not give any reliable assistance to the subject of the perforation of the cell-wall by protoplasmic threads.

When the protoplasm separates from the cell-wall in consequence of the action of dehydrating agents, it always tends to assume a spheroidal form, in consequence of the action of the two forces of pressure and tension, which endeavour to bring about a state of equilibrium. Now the pulling force that the living protoplasm must exhibit in contracting from the cell wall and assuming its spheroidal condition must be very considerable. As we have seen from the appearance presented by such sections as Plate 70, fig. 40, there is a tendency on separation for the protoplasm to adhere rather to the main protoplasmic mass than to the cell-wall, and in consequence of this the protoplasm of the fine filaments going through the cell-wall will tend to be pulled out of its canal, and thus the thread proceeding from it will be no thicker than one which arises from the general cell-wall, and will therefore not be especially apparent. In instances where plasmolysis is very rapidly induced, the protoplasm quickly contracts, and even becomes divided up into several masses. Then it may possibly happen that, owing to the particular combination of forces, a minute sphere of protoplasm may be retained, sticking to the pit membrane (as in Plate 70, fig. 34), although it may equally well adhere to the cell-wall (as in Plate 70, fig. 35).

But with such strong reagents as sulphuric acid the case is different. Owing to the rapid death of the protoplasm, the assumption of that spheroidal form attended with the exhibition of the usual rending force between the protoplasm and the cell-wall is prevented. The factor of life no longer asserts itself, and the contraction produced is now merely a mechanical shrinking, in consequence of dehydration, and the separation tends to take place rather between protoplasm and cell-wall than between protoplasm and protoplasm. Thus any intimate union which may exist between the protoplasm of the cell and the protoplasm running through the cell-wall tends to be maintained, and if sufficiently pronounced is made evident.*

I am now in a position to bring my paper to a conclusion.

I have succeeded in demonstrating that in living tissues a means of communication between adjacent cells exists. My results have been confirmed by Russow, whose valuable contribution I have already mentioned. The wide field that this discovery opens is so great, and the whole bearing of the subject is so enormous, that it would be useless for me either to attempt to sketch its significance or indicate the important inferences which arise therefrom, in the present paper. We are now in a position if not to understand, at least to get a clearer insight into, such phenomena as the downward movement of a sensitive leaf upon stimulation, of the wonderful action of a germinating embryo on the endosperm cells, even those which are far

* In connexion with this subject, see De Bary's figure of the sieve-tube of *Vitis* after the action of iodine and potassic iodide (*loc. cit.*, fig. 75, p. 186).

removed from it, and finally of the whole cell mechanism. The passage of protoplasm from cell to cell, which numerous observations have showed must occur, can now be explained, and the mere fact of the possibility of this taking place increases very materially our knowledge as to general mechanics of the vegetable cell.

Although I am aware of the danger of rushing to conclusions, I cannot but remark that when these results—which were foreshadowed by SACHS and HANSTEIN when they discovered the perforation of the sieve-plate—are taken in connexion with those of RUSSOW, it appears extremely probable that not only in the parenchymatous cells of pulvini, in phloem parenchyma, in endosperm cells, and in the prosenchymatous bast-fibres, is continuity established from cell to cell, but that the phenomena is of much wider, if not of universal occurrence.

Finally, I have to acknowledge the many kindnesses I have received during this investigation. Of Professor SACHS' kindness to me it is impossible for me to speak sufficiently highly. The mere fact that it was at his suggestion that this work was undertaken will show how much I owe him. To my friend and former teacher, Dr. S. H. VINES, I am indebted for much valuable advice. Especially must I also express my most sincere gratitude to my friend, Dr. D. H. SCOTT, not only for his valuable criticisms and suggestions, but for the many assistances that he has given me in every possible way during the whole of this difficult work.

NOTE.

(Added January 12th, 1884.)

Since the communication of the above I have written two more papers on the same subject, viz.:

1. "On the Continuity of the Protoplasm through the Walls of Vegetable Cells," Proc. Roy. Soc., December 20, 1884, which deals with the confirmation of my methods and the further establishing of my results. Since in the endosperm cells of *Bentinckia Conda-panna* the threads can be seen by merely mounting a section in dilute glycerine, such a preparation is taken as normal, and can be then compared with similar sections, in the preparation of which reagents have been employed. Such comparison is in every way satisfactory. I have further confirmed the existence of a continuity in *Dioncea*, and have established that in the parenchymatous cells of the leaf bases of *Aucuba Japonica* and *Prunus lauro-cerasus* distinct threads can be made out, crossing the pit-closing membrane. I then make some remarks as to the function of the threads.

2. "On the Continuity of the Protoplasm through the Walls of Vegetable Cells," Arbeiten des Botanischen Instituts in Würzburg. Bd. III., Heft I.

This is a fairly complete paper, embodying all the results I have obtained up to the present time.

Description of Plates.

PLATE 68.

Fig. 1. Transverse section of the pulvinus of *Trifolium repens* which in its principal details resembles that of *Mimosa pudica*. (× 55.)

Fig. 2. Longitudinal section of a portion of the pulvinus of *Trifolium repens*, showing the cells immediately beneath the epidermis. (× 105.)

Fig. 3. Longitudinal section of a portion of the pulvinus of *Mimosa pudica*, showing the cells immediately beneath the epidermis. The intercellular spaces are small and badly developed. (× 235.)

Fig. 4. Cells of the pulvinus of *Mimosa pudica* which are situated immediately around the vascular bundle. The intercellular spaces are large and conspicuous. (× 235.)

Fig. 5. Cells of the pulvinus of *Mimosa pudica*, situated midway between the epidermis and the vascular bundle, after treatment with sulphuric acid, staining with methyl violet, and washing with dilute glycerine. The protoplasmic contents are shrunken and deeply coloured. The remains of the middle lamellæ can be seen. Certain of the processes appear to join uninterruptedly from cell to cell. In others between the two darkly stained ends is a lighter stained area uniting the two. The latter is believed to be the typical and only true means of continuity. (× 550.)

Fig. 6. Portions of two bast-cells from the pulvinus of *Mimosa pudica* after treatment with sulphuric acid, and staining with methyl violet and glycerine. (× 1020.)

Fig. 7. Cells of the pulvinus of *Robinia pseudacacia*, situated as in *Mimosa* (fig. 5), after treatment with sulphuric acid and staining with methyl violet and glycerine. The typical mode of connexion between adjacent cells is better seen than in *Mimosa*. The appearances of an uninterrupted continuity are not so frequent. (× 550.)

Fig. 8. Cells of the pulvinus of *Robinia pseudacacia* after treatment with sulphuric acid and staining with methylene blue. The bottom and sides of the pits are stained. (× 105.)

Fig. 9. Longitudinal section of a portion of the pulvinus of *Amicia zygomeris*. In certain of the cells conspicuous pits are apparent. (× 235.)

Fig. 10. Cells of the pulvinus of *Amicia zygomeris*, situated midway between the epidermis and the vascular bundle, after treatment with sulphuric acid, staining with methyl violet, and mounting in dilute glycerine. Between the adjoining masses of the much shrunken protoplasm are numerous fine stained processes uniting the two. These in reality represent the stained

bottoms and sides of the much swollen and resistent pits. The swollen cell-wall abuts directly on to the protoplasm. By long treatment with dilute glycerine all the colour becomes dissolved from the pits, and the protoplasmic masses are then left fairly isolated one from another, or by prolonged treatment with sulphuric acid the resistent pits become swollen, and then stain like the rest of the wall. (× 1020.)

Fig. 11. Cells of the pulvinus of *Amicia zygomeris* situated immediately around the vascular bundle, where the cell-walls are thick and the pits deep and well developed, after treatment with sulphuric acid and staining with methyl violet and glycerine. The protoplasmic processes tend to adhere to the pit-membrane, and between any two contiguous processes is a lighter stained area. (× 1020.)

Fig. 12. A cell from the rachis of the leaf of *Cycas revoluta*, treated with iodine and Chlor. Zinc Iod. The pits opposite the intercellular spaces stain deep blue, whereas those separating the contents of adjacent cells are but feebly coloured. (× 235.)

PLATE 69.

Fig. 13. A cell from the ripe endosperm of *Phœnix dactylifera* after treatment with sulphuric acid and staining with methyl violet and glycerine. Some portions of the wall remain but little acted upon. The protoplasmic processes of the main shrunken mass have separated with difficulty from the pit-closing membrance, and the protoplasmic threads which traverse that structure, and normally abutted on to the ends of the protoplasmic processes of the pits, are well stained and brought into view. Compare figs. 6 and 11. (× 550.)

Fig. 14. Young endosperm cell of the seed of *Archontophœnix Cunninghamii* (*Seaforthia elegans*) after treatment with sulphuric acid and staining with methyl violet and glycerine. The pit processes of adjacent cells are united by fine protoplasmic threads, after the manner of a sieve-tube. This compares with figs. 5 and 7. (× 550.)

Fig. 15. Young endosperm cell of *Rhopalostylis sapida* (*Areca sapida*) after treatment with sulphuric acid, methyl violet, and glycerine. The processes from the shrunken protoplasm which enter the pits adhere to the pit-closing membrane, and the opposite processes of adjacent cells are united to one another and held in position by delicate protoplasmic threads perforating the pit-closing membrane. (× 550.)

Fig. 16. Cells of the ripe endosperm of *Bentinckia Conda-panna* after treatment with Chlor. Zinc Iod. and staining with picric-HOFMANN'S-blue. The proto-

plasmic cell contents have undergone degeneration, and many oil drops are present. Traversing both the thick pit-closing membranes, and also the general cell-walls, are complexes of fine protoplasmic threads. (× 550.)

Fig. 17. Portions of cells of ripe endosperm of *Howea Belmoreana* (*Kentia Belmoreana*), cell contents not shown, treated with Chlor. Zinc Iod. and picric-HOFMANN'S-blue. The threads traverse the pit-closing membranes and the general cell-walls. (× 550.)

Fig. 18. Cells of ripe endosperm of *Howea Belmoreana*, with protoplasmic cell contents. Treated as before. (× 550.)

Fig. 19. Portions of cells of the ripe endosperm of *Lodoicea Sechellarum* (the double cocoa-nut) treated with iodine and Chlor. Zinc Iod. Protoplasmic threads traverse the pit-membranes and general cell-wall. Cell contents not shown. (× 550.)

Fig. 20. Piece of cell-wall of same mounted in a mixture of iodine and glycerine. Threads fainter. Those traversing the unpitted portion of the wall do not appear to perforate as far as the free surface. The delicate channels containing protoplasm are widest in the region of the middle lamella, and colour with little or no swelling. In consequence of incomplete swelling the remaining portions of the threads are not visible. (× 550.)

Fig. 21. Portions of cells of the ripe endosperm of *Oncosperma horridum* treated with iodine and Chlor. Zinc Iod. The threads are very fine; much finer than it is possible to represent them in a drawing. (× 550.)

Fig. 22. Cells of the ripe endosperm of *Heterospathe elata* treated with Chlor. Zinc Iod. and picric-HOFMANN'S-blue. Middle lamella but little developed. Threads fairly thin. (× 550.)

Fig. 23. Portion of same treated with iodine and Chlor. Zinc Iod., showing that by such treatment the threads appear much thicker, owing to the precipitation of iodine upon them. (× 550.)

Fig. 24. Ripe endosperm cell of *Calamus callicarpus* treated with Chlor. Zinc Iod. and picric-HOFMANN'S-blue. Cell contents in this and many following omitted. Middle lamella well developed. Embedded in the cell-wall are crystals of calcium oxalate. (× 550.)

Fig. 25. Portions of ripe endosperm cells of *Syagrus botryophora* treated as before. Pits shallow and little developed. (× 550.)

PLATE 70.

Fig. 26. Cell of ripe endosperm of *Phytelephas macrocarpa* (vegetable ivory) treated with iodine and Chlor. Zinc Iod. (× 550.)

Fig. 27. Portion of cell-wall of almost ripe endosperm of *Bomarea oligantha* treated with Chlor. Zinc Iod. and picric-HOFMANN'S-blue. In the case of one of the pit-closing membranes the badly developed threads are not present over the whole of its surface. (× 550.)

Fig. 28. *En face* view of same. In the upper of the two pits the threads run as in the last described example. In the lower they are distributed equally over the surface. The figure is badly drawn, for in the upper pit the sections of the threads should have been more plainly apparent, and in the lower the unstained portions should have been represented stained, and *vice versâ*. (× 1020.)

Fig. 29. Portion of cell-walls of ripe endosperm of *Ruscus aculeatus* treated with Chlor. Zinc Iod. and picric-HOFMANN'S-blue. Pit-membranes thin. Threads badly developed and seen with difficulty. (× 550.)

Fig. 30. Portion of cells of ripe endosperm of *Colchicum speciosum* treated as before. Threads much better defined. (× 550.)

Fig. 31. Portion of cell-walls of ripe endosperm of *Asperula odorata* treated with iodine and Chlor. Zinc Iod. Threads traverse pit-membranes and walls. (× 550.)

Fig. 32. Portion of cell-walls of ripe endosperm of *Nemophila parviflora* treated with Chlor. Zinc Iod. and picric-HOFFMANN'S-blue. Cells small. Pit-membranes thin. Threads difficult to see. (× 550.)

Fig. 33. Portion of cell-walls of ripe endosperm of *Tamus communis* treated with iodine and Chlor. Zinc Iod. Part of the wall much swollen and coloured blue, in consequence of the usual cellular reaction. In this swollen area the threads can no longer be detected. In the lower half of the figure the apparently unswollen walls are commencing to swell, and the protoplasmic threads are breaking up into small points, instead of presenting the appearance of lines, as in the walls of the upper half of the section, which are still fairly intact. (× 550.)

Fig. 34. Cell of pulvinus of *Robinia pseudacacia* after treatment with a 10 per cent. solution of common salt. Appearance presented some two hours after plasmolysis. Certain of the threads can be seen going to pits. (× 550.)

Fig. 35. Cell of same tissue examined about ten minutes after mounting in 10 per cent. salt solution. (× 550.)

Fig. 36. Similar cell treated in the same way. Examined half an hour after treatment. (× 550.)

Fig. 37. Cells of pulvinus of *Apios tuberosa* treated with 5 per cent. salt solution. Examined three hours after plasmolysis. (× 440.)

Fig. 38. Cells of pulvinus of *Apios tuberosa* after treatment with 10 per cent. salt solution, saturated watery picric acid, and HOFMANN'S blue. Some of the threads are fairly preserved. Two thick threads appear to perforate

two pits, and unite the protoplasmic masses of the neighbouring cells as stated in text (refer to paper). (× 550.)

Fig. 39. Cell of the lamina of *Trichomanes pyxidiferum* as seen ten minutes after plasmolysis with a 10 per cent. salt solution (after BOWER). The threads appear to have no fixed relation to the pits. (× 550.)

Fig. 40. Similar cell as seen two hours after plasmolysis (after BOWER). (× 550.)

XXVI. *Supplement to former Paper, entitled—"Experimental Inquiry into the Composition of some of the Animals Fed and Slaughtered as Human Food."—Composition of the Ash of the entire Animals, and of certain separated parts.*

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In our former paper (Phil. Trans., Part II., 1859), we considered the analytical results which had then been obtained illustrating the actual and comparative composition of certain collective portions, and of the entire bodies, of animals of the farm, of different descriptions, and in different stages of growth and fatness. The results were given relating to ten animals, namely—a fat calf, a half-fat ox, a fat ox, a fat lamb, a store sheep, a half-fat old sheep, a fat sheep, a very fat sheep, a store pig, and a fat pig. The constituents which had been determined were—the total fat (by melting, expression, and ether-extraction), the total nitrogen, and the total mineral matter (ash). These were given in detail for certain separated parts, and in summary for all those parts collectively which are usually classed by the butcher as "carcass," for all those collectively classed as "offal," and for the entire animal (fasted live-weight). At that time the analyses of the ashes of the different animals, and their separated parts, were not completed. It is the object of this supplementary paper to record the results of forty complete ash-analyses, and to indicate their connexion with the main inquiry, and their importance as an element of it. To do this it will be desirable in the first place briefly to summarise the results and conclusions previously given.

From the data above referred to, the composition of some of the separated parts, and of the entire bodies, of the ten animals was given, so far as the total mineral matter, the total nitrogenous substance, the total fat, the total dry substance, and the water are concerned.

From these results the composition of the increase in weight, during the fattening period, of numerous animals was estimated. Also, in numerous cases in which the amount and the composition of the food consumed had been determined, the relation of the constituents stored up in the increase to those so consumed was calculated. Finally, the relation of the non-nitrogenous, or non-flesh forming, to the nitrogenous constituents in animal food and in bread was compared.

For the study of the subject from a more physiological point of view, the actual weights, and the percentage proportion in the entire body, of the individual organs, and

of certain more arbitrarily separated parts, were determined. To this end in all 326 animals were experimented upon—namely, 2 calves, 2 heifers, and 14 oxen; 249 sheep, in five classes as to age, maturity, fatness, and mode of feeding; and 59 pigs, in seven classes, arranged chiefly according to the food consumed. The following is a very condensed summary of some of the results obtained in this part of the inquiry:—

TABLE I.—Percentage (in fasted live-weight) of certain collective parts.

	Oxen.	Sheep.	Pigs.
Stomachs and contents	11·61	7·43	1·28
Intestines and contents	2·74	3·53	6·24
Total	14·35	10·96	7·52
Heart and aorta, lungs and windpipe, liver, gall bladder and contents, pancreas and spleen	2·96	3·30	3·01
Blood	4·01	3·97	3·63
Total	6·97	7·27	6·64

These facts are of considerable interest viewed in connexion with the great difference in the character of the food of the different animals; the ruminants consuming such a large proportion of fibre, much of which is indigestible; and the well-fed pig but little indigestible matter, and a relatively large proportion of starch, the primary transformations of a large part of which are supposed to take place after leaving the stomach, and more or less throughout the intestinal canal. With the great variations which the figures show in the proportion of the receptacles and first laboratories of the food, with their contents, the further elaborating organs (if we may so say), with their fluids, appear to bear a much more uniform relation by weight to the entire body in the different descriptions of animal.

The results further showed that whilst during the fattening process the total "carcass" parts increased both in actual weight and in percentage in the entire body, the remaining parts, constituting the so-called "offal," also increased in actual weight, but in a much less degree than the carcass parts, and they actually diminished in percentage proportion to the total live-weight.

The following is a summary of the composition of the ten animals analysed:—

TABLE II.—Summary of the Composition of the Ten Animals Analysed.

	Mineral matter (Crude ash).	Dry nitrogenous substance.	Fat.	Total dry matter.	Water.	Contents of stomachs and intestines (in moist state).
PER CENT. IN CARCASS.						
Fat Calf	4·48	16·6	16·6	37·7	62·3	
Half-fat Ox	5·56	17·8	22·6	46·0	54·0	
Fat Ox	4·56	15·0	34·8	54·4	45·6	
Fat Lamb	3·63	10·9	36·9	51·4	48·6	
Store Sheep	4·36	14·5	23·8	42·7	57·3	
Half-fat old Sheep	4·13	14·9	31·3	50 3	49·7	
Fat Sheep	3·45	11·5	45·4	60·3	39·7	
Very fat Sheep	2·77	9·1	55·1	67·0	33·0	
Store Pig	2·57	14·0	28·1	44·7	55 3	
Fat Pig	1·40	10·5	49·5	61·4	38·6	
PER CENT. IN OFFAL (SUM OF PARTS EXCLUDING CONTENTS OF STOMACHS AND INTESTINES).						
Fat Calf	3·41	17·1	14·6	35·1	64·9	
Half-fat Ox	4·05	20·6	15·7	40·4	59·6	
Fat Ox	3·40	17·5	26·3	47·2	52·8	
Fat Lamb	2·45	18·9	20·1	41·5	58·5	
Store Sheep	2·19	18·0	16·1	36·3	63·7	
Half-fat old Sheep	2·72	17·7	18·5	38·9	61·1	
Fat Sheep	2 32	16·1	26·4	44·8	55·2	
Very fat Sheep	3·64	16·8	34·5	54·9	45·1	
Store Pig	3·07	14·0	15·0	32·1	67·9	
Fat Pig	2·97	14·8	22·8	40·6	59·4	
PER CENT. IN ENTIRE ANIMAL (FASTED LIVE-WEIGHT).						
Fat Calf	3·80	15·2	14·8	33·8	63·0	3·2
Half-fat Ox	4·66	16·6	19·1	40·3	51·5	8·2
Fat Ox	3·92	14·5	30·1	48·5	45·5	6·0
Fat Lamb	2·94	12·3	28·5	43·7	47·8	8·5
Store Sheep	3·16	14·8	18·7	36·7	57·3	6·0
Half-fat old Sheep	3·17	14·0	23·5	40·7	50·2	9·1
Fat Sheep	2·81	12·2	35·6	50·6	43·4	6·0
Very fat Sheep	2·90	10·9	45·8	59·6	35·2	5·2
Store Pig	2·67	13·7	23·3	39·7	55·1	5·2
Fat Pig	1·65	10·9	42·2	54·7	41·3	4·0

We must refer to our former paper for the detailed discussion of the composition of the animals, and their different parts, of which the foregoing Table gives a very

condensed view. We need only call attention here to some of the most prominent indications.

It will be observed that there is a very much larger proportion of total fat than of total nitrogenous substance, in all the animals excepting the calf; that the percentage of nitrogenous substance diminishes, and that of the fat greatly increases, as the animals mature; also that the percentage of the total mineral matter decreases as the animals mature.

It is obvious that the increase during the fattening period will consist in still less proportion of nitrogenous substance, and in still greater proportion of fat. In fact the amount of fat stored up may be 8 or 10 times as much as that of the nitrogenous substance; and in the case of very fat pigs even more. The proportion of the total mineral matter, like that of the nitrogenous substance, is also much less in the fattening increase of the animal, than in the entire body.

Calculation further showed that the proportion of the nitrogenous substance of the food which was finally retained was very small. For example, sheep fattening on a good mixed ration will probably so retain in increase less than 5, or even less than 4 per cent. of the nitrogenous substance consumed in their food. If, however, the food is low in nitrogenous substance, more than 5 per cent. of that consumed may be stored up. In the case of pigs a larger proportion of the nitrogenous substance of the food is stored up, perhaps on the average 7½ per cent. If the food be low in nitrogen, consisting chiefly of cereal grain for example, perhaps nearly 10 per cent., or if high in nitrogen perhaps not more than 5 per cent. of that consumed will be finally retained.

The amount of fat stored up was shown to be very much greater than the amount of ready formed fat in the food. Fat was, therefore, largely formed within the body; and the results led to the conclusion that it was largely produced from carbohydrates.

It has been stated that the amount of mineral matter stored up in fattening increase is very small. Further, the proportion of that consumed which is retained depends so much on the character of the food that no general estimate can be safely given. The amount is at any rate almost immaterial, and the proportion will probably be always considerably less than that of the consumed nitrogenous substance retained. In connexion with this point it may be mentioned that in the case of each of the oxen and sheep the amount of mineral matter to one of nitrogenous substance was almost exactly 0·3 in the collective carcass parts, but it was lower in the other parts, and in the entire bodies. The results which it is the special object of the present communication to put on record will throw more light on the mineral composition of the animals.

Before closing this summary statement, and entering upon the special subject-matter of the present paper, brief reference should be made to some conclusions of importance to which the consideration of the composition of the animals as so far given, led.

It was estimated that of the total nitrogenous substance, and of the total fat, of the bodies of the animals, the following proportions would be consumed as human food :—

TABLE III.

	Per cent. consumed as human food.	
	Of the total nitrogenous compounds of the body.	Of the total fat of the body.
Calves	60	95
Oxen	60	80
Lambs	50	95
Sheep	50	75
Pigs	78	90

Thus, not only do the bodies of the fattened animals contain much more fat than nitrogenous substance, but a much larger proportion of the total fat than of the total nitrogenous substance is estimated to be consumed as human food. It results that, taking the average of the fat and the very fat animals, nearly four times as much dry fat as dry nitrogenous substance would be so consumed.

Finally, a comparison of the composition of the estimated consumable portions of the fattened animals, with that of wheat-flour bread, led to the conclusion that, taking into consideration the much higher oxidable capacity of the fat of the animal food than of the starch of the bread, the animal food contributed a considerably higher proportion of non-nitrogenous substance, reckoned as starch, to one of nitrogenous substance, than bread. We said :—"It would appear to be unquestionable, therefore, that the influence of the introduction of our staple animal foods, to supplement our otherwise mainly farinaceous diet, is, on the large scale, to reduce, and not to increase, the relation of the assumed flesh-forming material, to the more peculiarly respiratory and fat forming capacity, so to speak, of the food consumed."

It was concluded that the admitted advantages of a mixed animal and vegetable diet were essentially connected with the amount, the condition, and the distribution of the fat in the animal portions of the food ; that concentration and digestibility were probably elements in the explanation of the facts ; that the liberal distribution of the ready-formed fat with the transforming nitrogenous matters throughout the body, will modify the character of the changes constantly going on ; and that the difference in the condition of the nitrogenous substance in the animal and vegetable foods, has also to be taken into account.

Quantity and Composition of the Mineral Matter (Ash) in certain separated parts, and in the entire bodies, of the ten animals analysed.

In our former paper the actual quantity of ash was given for the bones, and for certain soft parts separately, of the carcass ; also for each separate internal organ, and

for other separated parts constituting the offal (Appendix-Tables I.–X., pp. 580–589); and the percentage of ash in each separated part is given in Appendix-Table XII., p. 591. At that time the ashes had not been analysed; but the work has now been long completed, and the results have only waited for leisure for adequate discussion. It is not proposed even now to treat the subject exhaustively, but to submit the results obtained with so much explanation and comment as will suffice to give a clear idea of their character, to indicate some of their most important bearings, and to direct the further study of them.

The ashes that have been analysed are, for each of the ten animals—1. Of a proportional mixture of all carcass parts; 2. Of a proportional mixture of all offal parts; 3. Of a proportional mixture of all parts, both carcass and offal, representing the ash of the entire animal.

As separated by the butcher, there is but little difference in the apportionment of the different parts to the carcass and offal respectively, in the case of oxen and sheep; but whilst with these animals the head and feet go with the offal, in the case of the pigs they are weighed with the carcass. Accordingly, the head and feet of the pigs were separately treated, and the ashes of these parts separately analysed. In the Tables, for the sake of comparison with the results for the other animals, those relating to the head and feet of the pigs are not included with the carcass; but they can, of course, be reckoned either with the carcass or with the offal as may be desired.

In the case of the oxen and sheep, the portions yielding carcass-ash are—the greater part of the skeleton, the flesh, the kidneys, and the fat membrane of the parts. In the case of the pigs the skin also is included with the carcass. The offal parts yielding ash are—the stomachs and intestines (without contents and washed), the heart, aorta, lungs, windpipe, blood, liver, pancreas, thymus gland, the glands about the throat, the spleen, the bladder, gall-bladder, bile, brains, tongue, head flesh, head bones, head skin and ears, pelt, hair or wool, leg bones, feet and hoofs, tail flesh, tail bones, diaphragm, &c.

Of the ashes from the carcass parts twelve complete analyses have been made; that is, one for the carcass of each of the ten animals, and two duplicates. The duplicates are of the fat ox, and of the fat sheep, carcass ashes.

Of the ashes from the offal parts, seventeen complete analyses have been made; one for the offal parts of each animal, one for the head and feet ash of each of the two pigs, and five duplicates.

Of the ashes representing the entire bodies of the animals, eleven analyses have been made; that is one for each animal, and one duplicate.

In all, therefore, forty complete ash analyses have been made; and there have frequently been duplicate determinations of individual constituents. The detailed results of the analyses are given in Appendix-Table I. (p. 885) for the ashes of the carcass parts; in Appendix-Table II. (p. 886) for the ashes of the offal parts; and in Appendix-Table III. (p. 887) for the entire animal ashes. In the upper division of each Table

the actual analytical results are given; in the middle division the same calculated to exactly 100; and in the lower division the results are calculated to 100 excluding sand and charcoal—that is, showing the composition of what may be called the *pure ash*.

In E. WOLFF's two volumes—'Aschen-Analysen'—he excludes carbonic acid, as well as sand and charcoal, in calculating the composition of what he terms "Reinasche." This exclusion could hardly be avoided in arranging for comparison the recorded results of various analysts, in many of which carbonic acid was not included; and from the point of view of the chemical statistics only, of crops and other products, it is of little consequence. As, however, in many cases, the amount of carbonic acid represents, more or less exactly according to circumstances, the quantity of base which has been in combination with organic acids, its amount, and the differences in its amount, in different descriptions of ash, are indications of considerable interest. Obviously, in the case of ashes of such heterogeneous mixtures as those now in question, the record is of less importance from this point of view; whilst in some of the animal matters carbonates doubtless exist as such. But, as in other cases it is important to include the carbonic acid among the constituents of the pure ash, it is included here also for the sake of uniformity of plan.

It is freely admitted that results relating to carbonic acid require very careful consideration, if misinterpretation is to be avoided. Not that the determination of the amount of it actually existing in an ash is a matter of difficulty in experienced hands; but, according to the character of the ash, and to the conditions of the incineration, more or less of the carbonates may have been converted into more fixed salts, or the carbonic acid may be expelled and the ash causticised.

It is in fact very difficult, if not impossible, with some descriptions of ash, such for example as contain much silica, or phosphates with less than three of fixed base, so to conduct the incineration as to retain what may be termed the normal amount of carbonic acid. Indeed, after an ash has been kept for some time, and has acquired water, and perhaps regained carbonic acid, it is in some cases extremely difficult finally to heat it before weighing out for analysis, so as to ensure, on the one hand the expulsion of all water, and on the other the retention of the normal amount of carbonic acid. These points have been very fully investigated in connexion with the analyses of about 700 ashes, of various products, of known history, prepared at Rothamsted.

In the ashes of the mixed animal matters the amount of carbonic acid is in all cases small; but the differences in the amounts obtained according to the methods of preparation for analysis well illustrate the difficulties involved. Thus, in five of the carcass ashes, and in eight of the entire animal ashes, carbonic acid was determined:—1, in the ash some time after preparation and without re-ignition (but calculated on re-ignited ash); 2, after re-ignition preparatory to weighing out for the determination of other constituents; 3, after treatment with ammonium carbonate and exposure to very low red heat. The average amount in the five carcass ashes was—determined in the not re-ignited ash 2·59, in the re-ignited ash 0·87, and in the ash treated with

ammonium carbonate and very gently heated 1·52; the average amount in the eight entire animal ashes was—determined in the not re-ignited ash 2·20, in the re-ignited ash 0·87, and in the ash treated with ammonium carbonate 1·48. After much comparative study of the results, the determinations after treatment with ammonium carbonate have been adopted throughout the series of animal ash analyses. Judging, however, from the recorded amounts of carbonates in numerous analyses of bones, and also from the analytical results themselves, as will be seen further on, it seems very probable that even the amounts so determined are too low. On the other hand, it is obvious that they are higher than in the ash in the re-ignited condition as weighed out for the determination of other constituents, and the generally high totals which the actual analyses show, are largely due to this cause. In fact, if the determinations of carbonic acid in the re-ignited ash had been entered in the Tables, not only would the totals have ranged considerably lower, but those for the carcass and entire animal ashes would range lower than those for the offal ashes, which is as it should be considering that fluorine was not determined in the ashes.

Thirty-seven of the forty animal ash analyses recorded in this paper were made, chiefly in the Rothamsted Laboratory, by Mr. RICHTER, now of Charlottenburg, Berlin; the remaining three were made by Mr. R. WARINGTON. Partly in the Rothamsted Laboratory and partly at Charlottenburg, Mr. RICHTER has conducted nearly the whole of the several hundred ash analyses above referred to, as well as numerous investigations of method, with a view to testing the limits of accuracy of previous work, and to attain greater accuracy in future. Besides the points already alluded to, he has analysed mixtures of precipitates obtained in precisely the same way in series of analyses, to determine their degree of purity, and so on. It is not intended to go into these matters of detail of method on this occasion. Satisfactory evidence will, however, be afforded in the course of the discussion of the results as to the degree of accuracy and trustworthiness of the analyses; and a comparison of the duplicates given in the Appendix-Tables I., II., and III. will afford further evidence on the point.*

Before considering the composition of the ashes it will be well to show at one view the amount, and to some extent the distribution, of the total ash in the different animals. The following Table (IV.) shows the amount of total ash in 100 fasted live-weight of each of the animals, and the proportion of the whole yielded by the carcass parts and the offal parts respectively. The first three columns show the amounts of crude ash, and the second three the amounts of pure ash. As already stated, the contents of stomachs and intestines are not included in the parts analysed.

* It need only further be remarked in reference to the analyses as such, that the subsequent investigations of method referred to above, lead to the conclusion that the phosphoric acid determinations made by the magnesium process (nearly the whole) may perhaps be too high, to an extent not exceeding 0·35 per cent. The actual results obtained are, however, recorded in the Tables; nor would any of the conclusions drawn be affected were the supposed correction adopted.

TABLE IV.—Percentage of Crude Ash, and of Pure Ash, in the fasted Live-Weight.

	Crude ash.			Pure ash.		
	From carcass parts.	From offal parts.	From total parts.	From carcass parts.	From offal parts.	From total parts.
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Fat Calf	2·782	1·018	3·800	2·772	1·006	3·779
Half-fat Ox	3·603	1·061	4·664	3·568	1·044	4·612
Fat Ox	3·019	0·901	3·920	2·997	0·882	3·879
Fat Lamb	2·173	0·763	2·936	2·162	0·719	2·881
Store Sheep	2·325	0·839	3·164	2·317	0·747	3·064
Half-fat Old Sheep	2·214	0·959	3·173	2·207	0·848	3·055
Fat Sheep	1·982	0·829	2·811	1·970	0·700	2·670
Very fat Sheep	1·748	1·155	2·903	1·744	1·123	2·867
Store Pig	1·708	0·961	2·669	1·699	0·954	2·652
Fat Pig	1·062	0·587	1·649	1·054	0·581	1·635

When referring to the amounts of crude ash as given in Table II., attention was called to the fact that the percentage of mineral matter, like that of the nitrogenous substance, decreases as the animals mature. This is more clearly seen in the figures in Table IV. relating to the pure ash. Thus, comparing the fat ox with the half-fat ox, there is not only a lower percentage of pure ash in the entire animal, but a lower proportion of the whole contributed both by the carcass parts and the offal parts. Comparing, again, the store sheep, the fat sheep, and the very fat sheep, there is a considerably lower percentage of mineral matter (pure ash) contributed from the carcass parts of the fat than of the store sheep, and less still from those of the very fat sheep. There is also less from the offal parts of the fat sheep than of the store sheep; but there is a considerable excess in the case of the offal parts of the very fat sheep; and, in consequence, some excess in the percentage in the entire animal. Lastly, comparing the store pig and the fat pig, the latter shows a considerably lower proportion of mineral matter from carcass parts, from offal parts, and from all parts.

Referring to the Appendix-Tables I., II., and III. (pp. 885-87), for any further details, the following Table, V., shows the percentage composition of the *pure ash* (that is, excluding sand and charcoal), of the classified parts and of the entire bodies of the ten animals analysed. The upper division of the Table gives the results for the ash of the carcass parts, the middle division for that of the offal parts, and the lower division for the ash of the entire bodies of the animals (excluding contents of stomachs and intestines). When duplicate analyses have been made the mean results only are here given. At the head of each division of the Table are given the percentages of crude ash and of pure ash, not as in Table IV. in each case calculated to the weight of the entire body, but to the weight of the collective parts to which the division refers.

It should be further explained that, for comparison with the results relating to the same parts of the other animals, the composition of the ash of the collective offal parts of the two pigs is calculated from the analyses of the ash of the parts exclusive of the head and feet, and of that of the head and feet, the details of which are given in Appendix-Table II. Again, it will be observed that the results relating to the entire animal ash of the very fat sheep are given in brackets, the figures not being those of the actual analysis, but calculated from the results of the analyses of the ash of the carcass parts and of the offal parts separately. The results of the actual analysis of the entire animal ash are given in the Appendix-Table III.; but although there is no reason to doubt the accuracy of the analysis, there can be no doubt that there has been some omission of parts in making the mixture for burning to ash. Some item rich in potash has obviously been omitted.

TABLE V.—Percentage of Crude Ash, and of Pure Ash (excluding Sand and Charcoal), and Percentage Composition of the Pure Ash.

	Fat Calf.	Half-fat Ox.	Fat Ox.	Fat Lamb.	Store Sheep.	Half-fat old Sheep.	Fat Sheep.	Very fat Sheep.	Store Pig.	Fat Pig.
COLLECTIVE CARCASS PARTS.										
	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.	Per cent.
Crude ash	4·48	5·56	4·56	3·63	4·36	4·13	3·45	2·77	2·57	1·40
Pure ash	4·46	5·51	4·53	3·61	4·34	4·12	3·43	2·76	2·56	1·39
Peroxide of iron	0·39	0·62	0·56	0·43	0·36	0·49	0·40	0·39	0·63	0·64
Lime	43·93	46·89	47·02	46·83	45·43	46·21	46·65	47·36	40·5	38·59
Magnesia	2·09	1·71	1·70	1·79	1·86	1·76	1·81	2·05	2·13	2·08
Potash	5·20	4·57	4·34	4·62	5·18	5·07	4·65	3·78	8·47	9·68
Soda	3·08	2·60	2·59	2·47	2·97	2·65	2·80	2·74	3·72	4·40
Phosphoric acid	41·54	40·00	40·40	40·37	40·36	40·62	40·84	41·00	40·02	40·19
Sulphuric acid	1·03	0·66	0·69	0·81	1·24	0·80	0·53	0·47	1·96	1·26
Carbonic acid	1·14	1·80	1·68	1·82	1·40	1·84	1·47	1·63	1·17	1·26
Chlorine	1·02	0·75	0·88	0·93	1·46	1·02	0·93	0·70	1·81	2·25
Silica	0·11	0·27	0·14	0·14	0·07	0·07	0·13	0·04	0·15	0·17
Total	100·23	100·17	100·20	100·21	100·33	100·23	100·21	100·16	100·41	100·52
Deduct O = Cl.	0·23	0·17	0·20	0·21	0·33	0·23	0·21	0·16	0·41	0·52
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
COLLECTIVE OFFAL PARTS (EXCLUDING CONTENTS OF STOMACH AND INTESTINES).										
Crude ash	3·41	4·05	3·40	2·45	2·19	2·72	2·32	3·64	3·07	2·97
Pure ash	3·37	3·98	3·33	2·31	1·95	2·40	1·96	3·54	3·04	2·93
Peroxide of iron	1·10	1·32	1·78	2·41	3·68	3·73	4·87	2·09	0·90	1·31
Lime	41·39	44·61	41·16	35·91	36·49	37·35	35·22	36·97	41·77	41·07
Magnesia	1·68	1·42	1·28	1·67	1·77	1·57	1·81	1·69	1·79	1·59
Potash	4·46	3·10	4·80	9·28	7·25	7·37	7·89	8·23	5·60	5·99
Soda	6·53	5·56	6·41	6·91	6·99	5·58	6·03	7·29	4·81	4·86
Phosphoric acid	39·26	38·12	39·27	34·86	33·60	35·24	33·15	35·07	40·87	39·85
Sulphuric acid	1·19	1·23	1·59	2·42	2·87	3·17	3·36	1·52	1·23	1·50
Carbonic acid	1·14	1·76	0·90	0·89	0·92	0·99	1·07	1·81	0·67	1·40
Chlorine	3·80	3·30	3·07	4·74	5·31	3·38	3·72	4·76	2·58	2·99
Silica	0·31	0·41	0·48	1·48	2·40	2·38	3·72	1·34	0·34	0·28
Total	100·86	100·73	100·69	101·07	101·21	100·76	100·84	101·07	100·56	100·84
Deduct O = Cl.	0·86	0·73	0·69	1·07	1·21	0·76	0·84	1·07	0·56	0·84
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
ENTIRE ANIMAL FASTED LIVE-WEIGHT (BUT CONTENTS OF STOMACH AND INTESTINES EXCLUDED).*										
Crude ash	3·80	4·66	3·92	2·94	3·16	3·17	2·81	2·90	2·67	1·65
Pure ash	3·77	4·61	3·88	2·88	3·06	3·06	2·69	2·86	2·65	1·64
Peroxide of iron	0·53	0·97	0·41	0·84	1·24	1·35	1·00	(1·05)	0·91	0·76
Lime	43·95	45·26	46·62	44·57	43·12	44·39	44·61	(43·29)	40·58	38·49
Magnesia	2·20	2·03	1·53	1·82	1·82	1·72	1·79	(1·90)	2·01	2·04
Potash	5·40	4·41	4·46	5·74	5·64	5·27	5·53	(5·53)	7·39	8·57
Soda	3·82	3·08	3·04	3·58	3·90	3·35	3·56	(4·52)	4·16	4·36
Phosphoric acid	40·37	40·22	39·80	38·96	38·96	39·15	38·72	(38·68)	40·12	40·14
Sulphuric acid	1·08	0·86	0·79	1·18	1·78	1·06	1·01	(0·99)	2·33	2·15
Carbonic acid	1·34	1·97	2·13	1·53	1·09	1·83	1·67	(1·70)	0·60	1·20
Chlorine	1·55	1·24	1·47	1·86	2·31	1·61	1·61	(2·30)	2·22	2·78
Silica	0·12	0·24	0·08	0·33	0·67	0·63	0·86	(0·56)	0·18	0·14
Total	100·36	100·28	100·33	100·41	100·53	100·36	100·36	(100·52)	100·50	100·63
Deduct O = Cl.	0·36	0·28	0·33	0·41	0·53	0·36	0·36	(0·52)	0·50	0·63
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00

* See p. 874, in reference to the entire animal ash of the very fat sheep.

The first point to notice in the analytical results is that the amount of iron peroxide is much higher in the ash of the offal parts than in that of the carcass parts, and that it is much higher in the offal ash of the sheep, than in that of either the oxen or the pigs. This is doubtless due to adventitious matter in the wool, which it was extremely difficult to clean. Indeed, alumina was found, clearly indicating the presence of ferruginous clay. Further, the amount of ferric oxide (as also that of silica) has a very obvious relation to the amount of "sand" found in the ashes. Notwithstanding, therefore, that the offal ash of the animals included that of the blood, the amount of ferric oxide found in the offal ashes must not be relied upon. Reference to Appendix-Table III. will show, however, that the ashes of the offal parts of the pigs, exclusive of the head and feet, do contain a very high percentage of ferric oxide; but if, as in the case of the oxen and sheep, the ash of the head and feet, with its very low percentage of ferric oxide, be included in the collective offal ash, the percentage of ferric oxide in the so-reckoned offal ash of the pig is much lower than in that of the sheep.

The records of the amounts of ferric oxide in the ashes of the carcass parts are only very little open to the same objection as in the case of the offal ashes; but it is obvious that the high percentage in the latter will unduly raise the amount in the entire animal ashes.

Referring to the more important constituents, it is at once seen that the animal ashes consist very largely of phosphate of lime. In the case of ashes of crude products, and particularly of mixed animal substances like those now under consideration, it would be out of place to attempt to arrange the constituents as salts. But it may nevertheless be useful to indicate the general relation of base to acid in the ashes. The lime and magnesia may be taken as essentially, though of course not exclusively, representing the bases of the bone-ash; whilst the potash and soda may in the same general, though not in an exclusive sense, be classified as the flesh and blood bases. Again, by far the larger proportion of the phosphoric acid will be due to the bones; whilst some of it as such, and probably some as the product of the oxidation of phosphorus in the burning, will be connected with the nitrogenous constituents in the non-bony portions of the body. The sulphuric acid, again, will in part be due to the oxidation of sulphur in the burning.

It may be stated, by way of illustration only, that if the phosphoric acid found be calculated as wholly tribasic, the lime of the ashes, excepting in the case of the pigs, would be nearly, and the lime and magnesia together, quite, or more than, sufficient to combine with the whole of the phosphoric acid. The potash and soda again, would be considerably more than sufficient to combine with the sulphuric acid, chlorine, and carbonic acid. It is thus indicated that, notwithstanding some of the phosphoric acid found may be due to the oxidation of phosphorus, and some of the sulphuric acid to the oxidation of sulphur, in the burning, there is upon the whole, according to the above mode of reckoning, an excess of base in the ashes of the

ruminants, whilst figures obtained in the same way do not indicate a similar result in the case of the pigs. In the ashes of the pigs the phosphoric acid is considerably in excess of the quantity required to give tribasic phosphates with the whole of the lime and magnesia; the former of which is in relative deficiency. The result is that, upon the whole ash of the pigs, the figures show a deficiency rather than an excess of base, especially in the case of the fatter animal.

The consistency of the result with the ruminants, and again the consistency, but in the opposite direction, with the pigs, would lead to the conclusion that the indication is not simply due to the conditions of incineration, or to error of any kind. As bearing upon the point it is in the first place to be borne in mind that fluorine was not determined in the ashes; but certainly its amount would not be sufficient to turn the scale. Then there is the question whether organic acid salts, and carbonates existing as such, are adequately represented by the amount of carbonic acid determined in the ashes; and there is the further question whether sulphuric acid, and possibly phosphoric acid, may have been reduced, or sulphuric acid or chlorine expelled, in the burning.

According to direct experiments of WAY and OGSTON (Jour. Roy. Ag. Soc. Eng., vol. ix.), sulphuric acid is expelled by silica, but not by acid phosphates, in incineration. They conclude, however, that there is no loss of phosphoric acid; nor of chlorine in careful burning. Others have concluded that the expulsion of both sulphuric acid and chlorine is dependent both on the character of the ash, and on the conditions of the incineration; and in this Mr. RICHTER'S experience leads him to concur. On the other hand it has to be considered whether the phosphoric acid and sulphuric acid found in the ashes are not in excess of the amounts existing as such in the substances burnt. On this point WAY and OGSTON and others have long ago concluded that sulphur is oxidated in incineration in very variable amounts according to circumstances; and quite recently GROUVEN has concluded that sulphur is converted into sulphuric acid in the ordinary methods of incineration in free air, and that under the same circumstances sulphates existing in the organic substance burnt are not reduced. GROUVEN concludes that about half of the sulphur may be converted into sulphuric acid in the burning. Again, according to Dr. VOELCKER'S experiments (Rep. Brit. Ass., 1857, abstract, p. 60) at any rate a large proportion of the sulphur and phosphorus is not oxidated in the incineration; and FRESENIUS has obtained similar results so far as phosphorus is concerned. Lastly, with regard to the question whether sulphuric acid is reduced by charcoal in the burning, Mr. RICHTER has found in some parallel experiments with wheat grain ashes high sulphuric acid with high charcoal, and low sulphuric acid with low charcoal; but on the other hand he has not observed sulphuretted hydrogen on dissolving such ashes in hydrochloric acid.

It may be stated that the foregoing observations as to the relation of base and acid in the ashes apply generally to those of the collective carcass, of the collective offal, and of the entire bodies of the different descriptions of animal. But where, as in the

case of the pigs, the ash of the head and feet, and that of the other offal parts, were analysed separately, the ash of the former, due largely to bone, showed some excess of base even calculating the whole of the phosphoric acid as tribasic, whilst the ash of the other offal parts (the soft parts, blood, &c.) showed, on the same mode of reckoning, about one and a half time as much acid as base; indeed of phosphoric acid alone there is, so reckoned, very much more than is equivalent to the total bases. Here then there is evidence that the ash of the soft parts contains phosphoric acid with less than three of fixed base, and probably some due to the oxidation of phosphorus. In further elucidation of the point in question it may be stated that, although the oxen and sheep show a higher percentage of total nitrogenous substance than the pigs, yet the amount of pure ash yielded from the non-bony parts is higher in proportion to that from the bones in the case of the pigs than in that of the ruminants. That is to say, there is with the pigs a higher proportion of the ash due to parts containing more potash and soda, and less lime and magnesia as base; and so far as phosphoric acid may have existed in the animal substance in combination with potash and soda as ortho-phosphates with water or ammonia also as base, the calculation of the whole of the phosphoric acid of the ash as tribasic (as in our illustration) would necessarily show a relative deficiency of base.

Examination of the Table will show, as might be expected, that the ash of the carcass parts contains a much higher percentage of potash than of soda. This is the case with both the ruminants and the pigs. But with the relative deficiency of lime in the carcass-ash of the pigs, there is a higher percentage of both potash and soda than in that of the ruminants. The distinction between the different animals on these points is chiefly due to the less proportion of ash from bone in the case of the pigs; but it may in part be due to the thick skin being included with the carcass in the case of the pigs, whilst in that of the other animals the skin is not so included.

The ash of the offal parts, including that of the blood, but comparatively little of that of bones, contains, in the case of the ruminants, generally a much higher percentage of both potash and soda than that of the carcass parts, but the proportion of soda to potash is much greater. In the offal ash of the pigs on the other hand (which does not include the ash of the skin) the percentage of both potash and soda is considerably lower than in that of the sheep, and the soda considerably lower than in that of the oxen also.

Reference to Appendix-Table II. (p. 886) will show that in the ash of the offal parts of the pigs excluding the skin and the head and feet, there is only between 3 and 4 per cent. of lime, but about 25 per cent. of potash, and nearly 15 per cent. of soda; whilst in the ash of the head and feet there is nearly 50 per cent. of lime, only between 1 and 2 per cent. of potash, and between 2 and 3 per cent. of soda. Again, as above referred to, there was a considerable excess of acid, especially phosphoric, in the ash of the non-bony portions.

Comparing the percentage composition of the ashes of the entire bodies of the

different animals, the chief points of distinction are that, in the case of the pigs there is a lower percentage of lime, a higher percentage of potash and soda, and a higher percentage of sulphuric acid than in the corresponding ash of the ruminants. There is also generally a somewhat higher percentage of phosphoric acid in the entire animal ash of the pigs and the oxen than in that of the sheep.

With these few remarks suggested by a consideration of the percentage composition of the different ashes, we turn now to the bearing of the results as brought to view on applying them to calculate the amount, and as far as practicable the distribution, of the several constituents in a given live-weight of the different animals.

Accordingly, there is given in Table VI. (p. 880), not as before the quantity in 100 of ash, but the quantity in lbs. of each ash constituent, in the actual weight of the collective carcass parts, in the actual weight of the collective offal parts, and in the actual weight of all parts of each of the ten animals. The results are given in more detail in the upper portions of Appendix-Tables IV., V., and VI. (pp. 888-90); in IV. for the calf and oxen, in V. for the lamb and sheep, and in VI. for the pigs. There will be found, besides the amounts in the carcass parts, and in the offal parts respectively, those in the entire animal—first, by addition of the quantities in the carcass and offal parts; secondly, calculated from the direct analysis of the entire animal ashes; and thirdly, the mean of the two last quantities. For the composition of the entire animal, as given in Table VI. (p. 880), this *mean result* is adopted.

Again, in Table VII. (p. 881), is given the quantity of each constituent, not in the actual weight of the separated parts, and the entire bodies of the animals, but calculated in each case to 1,000 lbs. fasted live-weight; thus giving a comparative view of the composition of a given live-weight of the different animals, so far as the mineral or ash constituents are concerned. The particulars are given in detail in the lower divisions of the Appendix-Tables IV., V., and VI.

In the Tables VI. and VII. (pp. 880-81), as in former ones, the upper division gives the results for the carcass parts, the middle division those for the offal parts, and the lower division those for all parts collectively.

Before commenting on these Summary-Tables, we would call attention to the close accordance which the Appendix-Tables IV., V., and VI. show in the mineral composition of the entire bodies, calculated in the one case by the addition of the constituents determined separately in the carcass and in the offal parts, and in the other from the direct analysis of the ash from all parts. It is to be observed that this accordance is satisfactory confirmation not only of the correctness of the ash analyses, but of the preparation of the proportional mixtures of the different parts for burning, representing, respectively, the collective carcass parts, the collective offal parts, and the mixture of all parts. The result of the comparison will, we think, be found very satisfactory in every case excepting that of the entire animal ash of the very fat sheep, to the probable source of error in which reference has already been made (p. 874).

TABLE VI.—Quantities, in lbs., of Pure Ash, and of each Ash Constituent, in the Collective Carcass Parts, in the Collective Offal Parts, and in the Entire Body (fasted live-weight) of each Animal.

	Fat Calf.	Half-fat Ox.	Fat Ox.	Fat Lamb.	Store Sheep.	Half-fat Old Sheep.	Fat Sheep.	Very Fat Sheep.	Store Pig.	Fat Pig.
COLLECTIVE CARCASS PARTS.										
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh weight	160·560	797·688	939·375	50·500	52·063	56·259	73·063	159·250	62·403	140·546
Pure ash	7·173	43·945	42·531	1·831	2·262	2·319	2·505	4·399	1·598	1·949
Peroxide of iron	0·027	0·275	0·240	0·008	0·008	0·011	0·010	0·017	0·010	0·012
Lime	3·151	20·606	19·998	0·857	1·027	1·071	1·169	2·033	0·645	0·752
Magnesia	0·150	0·754	0·724	0·033	0·042	0·041	0·045	0·090	0·034	0·041
Potash	0·423	2·139	1·932	0·085	0·117	0·117	0·117	0·166	0·135	0·139
Soda	0·221	1·141	1·105	0·045	0·067	0·061	0·070	0·120	0·060	0·085
Phosphoric acid	2·980	17·574	17·174	0·739	0·913	0·942	1·028	1·804	0·640	0·788
Sulphuric acid	0·074	0·293	0·296	0·015	0·027	0·012	0·013	0·021	0·031	0·025
Carbonic acid	0·082	0·790	0·715	0·033	0·032	0·043	0·037	0·072	0·019	0·025
Chlorine	0·073	0·328	0·373	0·017	0·033	0·024	0·023	0·031	0·029	0·044
Silica	0·008	0·120	0·060	0·003	0·002	0·002	0·003	0·002	0·002	0·003
Total	7·189	44·020	42·617	1·835	2·269	2·324	2·510	4·406	1·605	1·959
Deduct O = Cl.	0·016	0·075	0·086	0·004	0·007	0·005	0·005	0·007	0·007	0·010
Total	7·173	43·945	42·531	1·831	2·262	2·319	2·505	4·399	1·598	1·949
COLLECTIVE OFFAL PARTS (EXCLUDING CONTENTS OF STOMACHS AND INTESTINES).										
Fresh weight	77·114	322·766	376·036	26·331	37·433	37·110	45·408	80·113	29·492	36·541
Pure ash	2·604	12·869	12·522	0·603	0·730	0·891	0·890	2·339	0·893	1·069
Peroxide of iron	0·029	0·170	0·223	0·015	0·027	0·033	0·043	0·059	0·008	0·014
Lime	1·077	5·728	5·153	0·217	0·266	0·333	0·313	1·050	0·373	0·439
Magnesia	0·044	0·183	0·161	0·010	0·013	0·014	0·016	0·048	0·016	0·017
Potash	0·116	0·399	0·601	0·056	0·053	0·066	0·070	0·231	0·050	0·064
Soda	0·170	0·715	0·302	0·042	0·051	0·050	0·054	0·207	0·043	0·052
Phosphoric acid	1·022	4·905	4·916	0·210	0·244	0·314	0·295	0·926	0·365	0·426
Sulphuric acid	0·031	0·160	0·200	0·021	0·021	0·028	0·030	0·051	0·011	0·016
Carbonic acid	0·030	0·226	0·113	0·002	0·007	0·009	0·010	0·051	0·006	0·016
Chlorine	0·099	0·425	0·385	0·028	0·039	0·030	0·033	0·135	0·028	0·032
Silica	0·008	0·052	0·054	0·009	0·018	0·021	0·033	0·038	0·003	0·003
Total	2·626	12·963	12·608	0·610	0·739	0·898	0·897	2·369	0·898	1·078
Deduct O = Cl.	0·022	0·094	0·086	0·007	0·009	0·007	0·007	0·030	0·005	0·009
Total	2·604	12·869	12·522	0·603	0·730	0·891	0·890	2·339	0·893	1·069
ENTIRE ANIMAL, FASTED LIVE-WEIGHT (BUT CONSTITUENTS OF CONTENTS OF STOMACHS AND INTESTINES EXCLUDED).*										
Fresh weight	258·750	1232·000	1419·000	84·406	97·625	105·063	127·156	239·363	92·938	185·000
Pure ash	9·765	56·818	55·094	2·438	2·991	3·217	3·411	7·238	2·491	3·022
Peroxide of iron	0·054	0·499	0·346	0·022	0·036	0·044	0·044	(0·076)	0·021	0·025
Lime	4·257	26·026	25·428	1·082	1·291	1·418	1·505	(3·183)	1·014	1·177
Magnesia	0·204	1·043	0·886	0·044	0·055	0·055	0·061	(0·138)	0·050	0·060
Potash	0·533	2·521	2·496	0·141	0·170	0·177	0·189	(0·400)	0·185	0·256
Soda	0·382	1·802	1·790	0·087	0·117	0·110	0·123	(0·327)	0·104	0·135
Phosphoric acid	3·969	22·668	22·015	0·950	1·161	1·259	1·322	(2·800)	1·002	1·211
Sulphuric acid	0·105	0·471	0·465	0·032	0·051	0·037	0·039	(0·072)	0·030	0·053
Carbonic acid	0·122	1·068	1·004	0·035	0·036	0·052	0·052	(0·123)	0·020	0·039
Chlorine	0·162	0·730	0·782	0·045	0·070	0·053	0·056	(0·166)	0·053	0·080
Silica	0·014	0·155	0·080	0·010	0·020	0·021	0·033	(0·040)	0·005	0·005
Total	9·802	56·983	55·272	2·449	3·007	3·229	3·424	(7·275)	2·504	3·041
Deduct O = Cl.	0·037	0·165	0·178	0·011	0·016	0·012	0·013	(0·037)	0·013	0·019
Total	9·765	56·818	55·094	2·438	2·991	3·217	3·411	(7·238)	2·491	3·022

* See p. 874, in reference to the entire animal ash of the very fat sheep.

TABLE VII.—Quantities, in lbs., of Pure Ash, and of each Ash Constituent, in 1,000 lbs. Fasted Live-Weight in each case.

	Fat Calf.	Half-fat Ox.	Fat Ox.	Fat Lamb.	Store Sheep.	Half-fat o'd Sheep.	Fat Sheep.	Very Fat Sheep.	Store Pig.	Fat Pig.
Collective Carcass Parts.										
Fresh-weight	lbs. 621	lbs. 647	lbs. 662	lbs. 598	lbs. 533	lbs. 536	lbs. 575	lbs. 630	lbs. 664	lbs. 760
Pure ash	27·742	35·643	29·973	21·682	23·158	22·094	19·715	17·402	17·008	10·539
Peroxide of iron	0·104	0·223	0·169	0·095	0·082	0·105	0·079	0·067	0·106	0·065
Lime	12·187	16·713	14·093	10·148	10·514	10·204	9·200	8·240	6·863	4·066
Magnesia	0·580	0·611	0·512	0·391	0·430	0·391	0·354	0·356	0·362	0·222
Potash	1·636	1·735	1·361	1·006	1·198	1·115	0·921	0·836	1·436	1·022
Soda	0·855	0·925	0·779	0·533	0·686	0·551	0·451	0·475	0·638	0·460
Phosphoric acid	11·326	14·254	12·103	8·751	9·847	8·974	8·051	7·136	6·810	4·284
Sulphuric acid	0·286	0·238	0·203	0·178	0·287	0·114	0·102	0·083	0·330	0·135
Carbonic acid	0·317	0·641	0·504	0·391	0·328	0·416	0·291	0·235	0·202	0·135
Chlorine	0·282	0·266	0·263	0·201	0·338	0·229	0·181	0·123	0·309	0·238
Silica	0·031	0·093	0·042	0·035	0·020	0·019	0·024	0·008	0·021	0·016
Total	27·804	35·704	30·034	21·729	23·230	22·142	19·754	17·429	17·077	10·593
Deduct O = Cl.	0·062	0·061	0·061	0·047	0·072	0·048	0·039	0·027	0·074	0·054
Total	27·742	35·643	29·973	21·682	23·158	22·094	19·715	17·402	17·003	10·539
Collective Offal Parts (excluding Contents of Stomachs and Intestines).										
Fresh weight	998	282	265	312	385	353	357	317	314	197
Pure ash	10·063	10·447	8·824	7·145	7·469	8·476	6·998	11·234	9·488	5·756
Peroxide of iron	0·112	0·138	0·157	0·177	0·276	0·314	0·338	0·234	0·086	0·076
Lime	4·162	4·650	3·631	2·571	2·722	3·168	2·461	4·155	3·960	2·363
Magnesia	0·170	0·148	0·114	0·118	0·133	0·133	0·126	0·190	0·170	0·091
Potash	0·448	0·324	0·424	0·664	0·542	0·628	0·550	0·226	0·532	0·344
Soda	0·657	0·580	0·565	0·498	0·522	0·476	0·425	0·819	0·457	0·280
Phosphoric acid	3·949	3·982	3·464	2·488	2·496	2·987	2·319	3·941	3·878	2·294
Sulphuric acid	0·120	0·130	0·141	0·249	0·215	0·266	0·236	0·202	0·117	0·087
Carbonic acid	0·116	0·184	0·080	0·024	0·072	0·086	0·079	0·202	0·064	0·080
Chlorine	0·383	0·345	0·271	0·382	0·399	0·285	0·259	0·534	0·245	0·172
Silica	0·031	0·042	0·038	0·107	0·184	0·200	0·259	0·150	0·032	0·017
Total	10·148	10·823	8·885	7·228	7·561	8·543	7·052	11·353	9·541	5·804
Deduct O = Cl.	0·085	0·076	0·061	0·083	0·092	0·067	0·054	0·119	0·053	0·048
Total	10·063	10·447	8·824	7·145	7·469	8·476	6·998	11·234	9·488	5·756
Entire Animal, Fasted Live Weight (but Constituents of Contents of Stomachs and Intestines excluded).*										
Fresh-weight†	919	909	927	910	916	889	932	947	978	957
Pure ash	37·750	46·094	38·826	28·876	30·615	30·634	26·836	28·636	26·501	16·320
Peroxide of iron	0·207	0·405	0·244	0·261	0·389	0·419	0·343	(0·301)	0·218	0·133
Lime	16·463	21·114	17·919	12·808	13·214	13·503	11·844	(12·395)	10·792	6·359
Magnesia	0·788	0·846	0·611	0·515	0·558	0·524	0·484	(0·546)	0·532	0·324
Potash	2·061	2·045	1·759	1·664	1·735	1·681	1·483	(1·582)	1·968	1·380
Soda	1·477	1·461	1·261	1·030	1·167	1·043	0·968	(1·294)	1·101	0·727
Phosphoric acid	15·349	18·390	15·514	11·257	11·883	11·988	10·401	(11·077)	10·660	6·544
Sulphuric acid	0·406	0·382	0·328	0·386	0·322	0·352	0·307	(0·285)	0·532	0·288
Carbonic acid	0·470	0·367	0·708	0·427	0·369	0·529	0·409	(0·487)	0·213	0·208
Chlorine	0·625	0·593	0·552	0·533	0·722	0·505	0·437	(0·657)	0·570	0·432
Silica	0·054	0·126	0·056	0·119	0·205	0·204	0·255	(0·158)	0·053	0·025
Total	37·900	46·228	38·952	29·009	30·774	30·748	26·934	(28·782)	26·634	16·423
Deduct O = Cl.	0·141	0·134	0·126	0·124	0·159	0·114	0·098	(0·146)	0·133	0·103
Total	37·759	46·094	38·826	28·876	30·615	30·634	26·836	(28·636)	26·501	16·320

* See p. 874, in reference to the entire animal ash of the very fat sheep.

† Excluding evaporation, and contents of stomachs and intestines.

Not much stress should be laid on the exact quantities of the total ash, or of the individual mineral constituents, in the actual weights of the particular animals analysed, as shown in Table VI., as the actual weights and condition of animals coming under similar designations may vary considerably. Subject to the reservation here implied, it may be stated that a calf weighing 160 lbs. carried off less than 10 lbs. of total mineral matter; oxen weighing from 1,200 to 1,400 lbs. from 55 to 60 lbs.; a fat lamb about 2½ lbs.; a store sheep under 3 lbs; a fat sheep from 3¼ to 3½ lbs.; and a very fat sheep of nearly 240 lbs. live-weight, twice as much, or more than 7 lbs. The pigs again, contained less than sheep in proportion to their weight.

The calf carried off about 4 lbs. phosphoric acid=between 8 and 9 lbs. of phosphate of lime, little more than half-a-pound of potash, and immaterial amounts of other mineral constituents. The oxen carried off between 22 and 23 lbs. phosphoric acid=less than 50 lbs. of phosphate of lime, and about 2½ lbs. of potash. The fat lamb carried off less than 1 lb. phosphoric acid=only about 2 lbs. of phosphate of lime, the store sheep and an ordinary fat sheep rather more=between 2½ and 3 lbs. phosphate of lime, whilst the amount of potash in any of these animals would only be from 2½ to 3 ounces. There would be proportionally greater variation in the actual weight of pigs sold off the farm than of sheep; and, for this reason, it is especially in their case, though it is so in that of the other animals also, better to consider the amount of mineral constituents lost to the farm in them in relation to a given live-weight rather than in the actual live-weight.

Table VII. which shows the amount of the different constituents in carcass, in offal, and in the entire body, *of* 1,000 *lbs. fasted live-weight*, of the different animals, is much more instructive.

In the first place 1,000 lbs. live-weight of calves or oxen is seen to carry off much more mineral matter than 1,000 lbs. live-weight of lambs or sheep, and 1,000 lbs. live-weight of pigs much less than sheep. In the particular cases in question, there were 46 lbs. of total mineral matter per 1,000 lbs. live-weight of the lean ox of less actual weight, and scarcely 39 lbs. in an equal weight of the fatter animal. The difference is in the right direction, but doubtless somewhat excessive; the fatter and heavier animal having actually less total mineral matter. Whilst 1,000 lbs. live-weight of oxen may thus contain 40 lbs. or even nearly 50 lbs. of mineral matter, the same weight of sheep will carry off only about 30 lbs. or less, and the same live-weight of pigs less still, and sometimes very much less. In all cases by far the larger proportion of the total mineral matter is in the collective carcass parts; and in the case of the pigs the proportion so distributed would be much greater than the Table shows, as there the head and feet are included with the offal, whilst in practice they are weighed with the carcass.

Referring to the amounts of the most important mineral constituents, whilst 1,000 lbs. live-weight of calves or oxen may carry off from 30 to 40 lbs. of phosphate of lime, the same weight of sheep would carry off only about 26 lbs. or less, and an

equal live-weight of pigs considerably less still. With each description of animal the quantity of phosphate is less in a given live-weight of the fatter than of the leaner individuals; and this is especially so in the case of the pigs. In round numbers it may be said that 1,000 lbs. live-weight of oxen will carry off only 2 lbs., or less, of potash; 1,000 lbs. of sheep from 1¾ to 1½ lb.; and 1,000 lbs. of pigs about the same; in each case the less, the fatter the animal. Of the potash, as of the phosphoric acid, by far the larger proportion of the whole is in the carcass parts. The constituent coming next in amount is soda; but with oxen the quantity in 1,000 lbs. live-weight does not reach 1½ lb., with sheep it is only about 1 lb., and with pigs about the same, or less in the fat condition.

It may be said with regard to each description of animal that a given live-weight will contain less of every constituent the more it is matured or fattened.

So far as the practical bearings of the subject are concerned, it will be seen that the production and sale of the animals of the farm carries off comparatively immaterial amounts of mineral constituents, but an equal weight of oxen more than the same weight of sheep, and an equal weight of sheep more than the same weight of pigs. Again, four-fifths of the whole, or even much more, will be phosphate of lime, and the amount of potash very small. The loss to the land, or to the manure from purchased food, will, however, be considerably more with growing than with only fattening animals.

It is obvious, indeed, that the amount of mineral constituents lost to the farm by mere fattening increase will be almost insignificant. We have elsewhere estimated that the *increase* of oxen and sheep over the final four or six months of the fattening period, will not contain more than about 1½ per cent. of mineral matter; that of pigs over the usually shorter period not more than 1 per cent., and in the case of very fat animals less still.

As conveying a somewhat more definite idea on the point, the amount of some of the most important mineral constituents that would be removed from an acre of fair average pasture and arable land, in animal increase and in some other products, may be compared. Such estimates can obviously be only approximate, and the quantities will be subject to considerable range of variation. Taking them as such, it may be stated in general terms that—of phosphoric acid an acre would lose more in milk, and four or five times as much in wheat or barley grain, or in hay, as in the fattening increase of oxen or sheep. Of lime the land would lose about twice as much in the animal increase as in milk, or as in wheat or barley grain, but, perhaps, not more than one-tenth as much as in hay. Lastly, of potash an acre would yield only a fraction of a pound in animal increase, six or eight times as much in milk, perhaps twenty or thirty times as much in wheat or barley grain, and more than one hundred times as much in hay.

The loss to the land in the animal increase is, in fact, chiefly in phosphate of lime, in amount varying from 5 to 10 lbs. per acre. In milk the loss is higher in phosphoric acid, less in lime, and more in potash. In wheat and barley grain the loss

of phosphoric acid is several times as great, and it is chiefly as phosphate of potash; whilst in hay the loss in phosphoric acid is much the same as in wheat or barley grain, but that of both lime and potash is very much greater than in any of the other products.

It is freely granted that the results which have been brought forward are calculated to suggest rather than to answer questions of interest from the point of view of the physiologist. He will ask why the selection of parts submitted to analysis was not more detailed. The answer must be that the agricultural aspects of the subject were necessarily those which guided the course of the investigation; and that, although it would have been carried out in more detail had it been practicable to do so, the pressure of other equally essential work has enforced the limitation which has been adopted. The execution of 40 complete ash-analyses is indeed a matter of no small labour; and however much we may regret that we have not been able to give a wider scope to the inquiry, we must be satisfied that the results do at least form a substantial contribution to the chemical statistics of the feeding of the animals of the farm for human food.

APPENDIX-TABLE I.—Percentage Composition of the Ash of the Collective Carcass Parts of Ten Animals.

	Fat Calf.	Half-fat Ox.	Fat Ox. Analysis 1.	Fat Ox. Analysis 2.	Fat Ox. Mean.	Fat Lamb.	Store Sheep.	Half-fat old Sheep.	Fat Sheep. Analysis 1.	Fat Sheep. Analysis 2.	Fat Sheep. Mean.	Very fat Sheep.	Store Pig.	Fat Pig.
1. Actual Analyses of Crude Ash.														
Iron peroxide	0·39	0·62	0·56	0·56	0·56	0·43	0·36	0·49	0·40	0·40	0·40	0·39	0·63	0·64
Lime	44·25	46·57	46·95	47·00	46·98	46·88	45·60	46·06	46·54	46·73	46·63	47·67	46·42	38·89
Magnesia	2·11	1·70	1·75	1·65	1·70	1·79	1·87	1·76	1·79	1·81	1·80	2·06	2·13	2·10
Potash	5·94	4·84	4·54	4·53	4·53	4·63	5·20	5·05	4·64	4·67	4·66	3·60	5·49	9·76
Soda	3·10	2·68	2·55	2·64	2·60	2·47	2·93	2·84	2·72	2·87	2·80	2·76	3·73	4·43
Phosphoric acid	41·85	39·72	40·42	40·29	40·35	40·42	40·51	40·51	40·77	40·99	40·83	41·28	40·09	40·50
Sulphuric acid	1·04	0·86	0·85	0·73	0·69	0·81	1·25	0·85	0·82	0·84	0·83	0·47	1·96	1·27
Carbonic acid	1·15	1·79	1·69	1·68	1·68	1·82	1·40	1·63	1·47	(1·47)	1·47	1·64	1·17	1·27
Chlorine	1·03	0·74	0·86	0·89	0·88	0·93	1·47	1·02	0·93	0·93	0·93	0·71	1·91	2·27
Silica	0·11	0·27	0·14	0·14	0·14	0·14	0·07	0·07	0·12	0·14	0·13	0·04	0·15	0·17
Sand	0·35	0·98	0·69	0·74	0·71	0·49	0·36	0·36	0·61	0·61	0·61	0·28	0·41	0·76
Charcoal	Trace	Trace	Trace	Trace	Trace	None	Trace	None	Trace	Trace	Trace	Trace	Trace	Trace
Total	101·32	100·47	100·79	100·85	100·82	100·81	101·07	100·25	100·51	101·06	100·79	101·08	100·99	102·06
Deduct O=Cl	0·23	0·17	0·19	0·20	0·20	0·21	0·33	0·23	0·21	0·21	0·21	0·16	0·41	0·52
Total	101·09	100·30	100·60	100·65	100·62	100·60	100·74	100·02	100·30	100·85	100·58	100·92	100·58	101·54
2. Composition of Crude Ash, Calculated to exactly 100.														
Iron peroxide	0·38	0·62	0·56	0·56	0·56	0·43	0·36	0·49	0·40	0·40	0·40	0·39	0·62	0·63
Lime	43·77	46·43	46·87	46·69	46·83	46·60	45·28	46·07	46·40	46·34	46·37	47·23	46·19	38·30
Magnesia	2·09	1·70	1·74	1·64	1·69	1·78	1·86	1·74	1·78	1·79	1·79	2·04	2·12	2·07
Potash	5·88	4·82	4·51	4·50	4·51	4·60	5·16	5·05	4·63	4·63	4·63	3·77	5·44	9·61
Soda	3·07	2·67	2·54	2·62	2·58	2·45	2·96	2·64	2·71	2·85	2·78	2·73	3·71	4·36
Phosphoric acid	41·40	39·60	40·16	40·03	40·09	40·18	40·21	40·50	40·65	40·54	40·59	40·90	39·86	39·89
Sulphuric acid	1·03	0·86	0·85	0·73	0·69	0·81	1·24	0·85	0·82	0·84	0·83	0·47	1·95	1·25
Carbonic acid	1·14	1·78	1·67	1·67	1·67	1·81	1·39	1·63	1·46	1·46	1·46	1·63	1·16	1·25
Chlorine	1·02	0·74	0·86	0·88	0·87	0·92	1·46	1·02	0·93	0·92	0·93	0·70	1·90	2·24
Silica	0·11	0·27	0·14	0·14	0·14	0·14	0·07	0·07	0·12	0·14	0·13	0·04	0·15	0·17
Sand	0·34	0·98	0·69	0·74	0·72	0·49	0·36	0·36	0·61	0·60	0·60	0·28	0·41	0·75
Charcoal	Trace	Trace	Trace	Trace	Trace	None	Trace	None	Trace	Trace	Trace	Trace	Trace	Trace
Total	100·23	100·17	100·19	100·39	100·29	100·21	100·33	100·23	100·21	100·21	100·21	100·16	100·41	100·32
Deduct O=Cl	0·23	0·17	0·19	0·20	0·20	0·21	0·33	0·23	0·21	0·21	0·21	0·16	0·41	0·32
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
3. Composition of Pure Ash (that is excluding Sand and Charcoal) Calculated to 100.														
Iron peroxide	0·39	0·62	0·56	0·56	0·56	0·43	0·36	0·49	0·40	0·40	0·40	0·39	0·63	0·64
Lime	43·93	46·89	47·00	47·04	47·02	46·83	45·43	46·21	46·69	46·92	46·80	47·36	46·35	38·59
Magnesia	2·09	1·71	1·75	1·65	1·70	1·79	1·86	1·76	1·80	1·81	1·81	2·05	2·13	2·08
Potash	5·90	4·87	4·54	4·54	4·54	4·62	5·18	5·07	4·65	4·68	4·66	3·78	5·47	9·64
Soda	3·08	2·69	2·55	2·64	2·59	2·47	2·97	2·85	2·73	2·86	2·80	2·74	3·72	4·40
Phosphoric acid	41·54	40·00	40·46	40·33	40·40	40·37	40·36	40·62	40·90	40·79	40·84	41·00	40·02	40·19
Sulphuric acid	1·03	0·86	0·85	0·73	0·69	0·81	1·24	0·85	0·82	0·84	0·83	0·47	1·96	1·26
Carbonic acid	1·14	1·80	1·68	1·68	1·68	1·82	1·40	1·64	1·47	1·46	1·47	1·63	1·17	1·26
Chlorine	1·02	0·75	0·86	0·89	0·88	0·93	1·48	1·02	0·93	0·93	0·93	0·70	1·91	2·25
Silica	0·11	0·27	0·14	0·14	0·14	0·14	0·07	0·07	0·12	0·14	0·13	0·04	0·15	0·17
Total	100·23	100·17	100·19	100·20	100·20	100·21	100·33	100·23	100·21	100·21	100·21	100·16	100·41	100·32
Deduct O=Cl	0·23	0·17	0·19	0·20	0·20	0·21	0·33	0·23	0·21	0·21	0·21	0·16	0·41	0·32
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00

APPENDIX-TABLE II.—Percentage Composition of the Ash of the Collective (and some separated) Offal Parts (excluding Contents of Stomachs and Intestines) of Ten Animals.

	Fat Calf.			Half-fat Ox.				Fat Ox.	Fat Lamb.	Store Sheep.	Lean Sheep.	Half-fat old Sheep.	Very fat Sheep.			Store Pig (excluding head and feet).			Fat Pig (excluding head and feet).	Head and feet.	
	Analysis 1.	Analysis 2.	Mean.	Analysis 1.	Analysis 2.	Analysis 3.	Mean.						Analysis 1.	Analysis 2.	Mean.	Analysis 1.	Analysis 2.	Mean.		Store Pig.	Fat Pig.
1. ACTUAL ANALYSES OF CRUDE ASH.																					
Iron peroxide	1·16	1·06	1·11	1·12	1·49	1·29	1·30	1·73	2·29	2·29	2·38	4·16	2·09	2·01	2·05	4·25	4·65	4·45	5·70	0·20	0·28
Lime	41·57	41·71	41·64	44·52	43·37	44·05	43·98	40·09	34·15	32·56	33·31	30·08	36·21	36·21	36·21	2·50	2·39	2·44	3·65	49·90	49·43
Magnesia	1·71	1·66	1·68	1·57	1·62	1·93	1·71	1·28	1·59	1·56	1·40	1·56	1·67	1·64	1·66	1·64	2·85	2·25	1·32	1·17	1·05
Potash	6·46	6·53	6·49	5·90	5·11	5·36	5·46	4·66	6·83	6·46	6·57	6·74	8·05	8·06	8·06	23·17	23·53	23·35	24·04	1·66	1·69
Soda	6·61	6·53	6·57	5·37	5·41	5·70	5·49	6·24	6·57	6·25	4·96	5·15	7·14	7·14	7·14	14·25	14·50	14·38	13·58	2·67	2·78
Phosphoric acid	39·47	39·53	39·50	37·80	37·28	37·91	37·66	39·25	33·16	30·04	31·43	28·32	34·32	34·36	34·34	38·24	38·16	38·20	34·02	41·19	40·98
Sulphuric acid	1·20	1·20	1·20	1·24	1·22	1·16	1·22	1·55	2·25	2·57	2·63	2·87	1·77	1·78	1·78	2·53	2·34	2·44	2·70	0·36	1·15
Carbonic acid	1·27	1·02	1·15	1·74	(1·74)	(1·74)	1·74	(0·66)	(0·27)	0·63	0·46	0·91	1·72	1·82	1·77	(0·00)	(0·00)	(0·00)	0·56	0·76	1·59
Chlorine	3·91	3·85	3·88	3·39	3·36	3·04	3·26	2·99	4·51	4·75	3·92	3·16	4·67	4·66	4·66	9·80	7·67	8·83	9·68	1·25	1·33
Silica	0·30	0·31	0·31	0·40	0·33	0·46	0·40	0·42	1·41	2·15	2·12	3·18	1·26	1·25	1·31	1·21	1·02	1·12	1·10	0·14	0·16
Sand	1·22	1·11	1·16	1·48	1·93	1·41	1·62	2·09	5·81	10·99	11·71	15·72	2·75	2·80	2·77	3·62	2·78	3·20	3·61	0·29	0·46
Charcoal	Trace	Trace	Trace	Trace	Trace	Trace	Trace	None	Trace	Trace	Trace	Trace	Trace	Trace	Trace	0·27	0·46	0·37	1·78	Trace	Trace
Total	102·77	102·81	102·64	101·68	100·86	100·89	101·14	100·17	101·84	101·46	101·58	101·98	101·75	101·75	101·75	102·76	102·03	102·39	102·44	100·40	101·61
Deduct O=Cl	0·86	0·87	0·87	0·72	0·76	0·69	0·72	0·67	1·02	1·06	0·66	0·72	1·05	1·05	1·05	2·21	1·78	2·00	2·66	0·28	0·30
Total	101·91	101·64	101·77	100·96	100·10	100·20	100·43	99·50	100·82	100·40	100·90	101·14	100·70	100·70	100·70	100·54	100·25	100·39	99·78	100·52	101·31
2. COMPOSITION OF CRUDE ASH, CALCULATED TO EXACTLY 100.																					
Iron peroxide	1·14	1·04	1·09	1·11	1·49	1·29	1·30	1·74	2·27	2·28	2·30	4·11	2·08	2·00	2·04	4·29	4·64	4·44	5·71	0·20	0·28
Lime	40·79	41·04	40·91	44·10	43·22	43·96	43·79	40·29	33·84	32·43	33·01	29·74	35·96	35·96	35·96	2·46	2·38	2·43	3·67	49·64	49·12
Magnesia	1·68	1·64	1·66	1·56	1·62	1·93	1·70	1·29	1·57	1·57	1·39	1·54	1·66	1·63	1·65	1·62	2·51	2·07	1·32	1·16	1·03
Potash	6·37	6·46	6·42	5·97	5·11	5·37	5·55	4·70	6·75	6·45	6·51	6·67	7·99	8·02	8·00	23·05	23·47	23·26	24·09	1·65	1·67
Soda	6·49	6·43	6·46	5·22	5·40	5·69	5·47	6·27	6·51	6·23	4·94	5·09	7·09	7·09	7·09	14·17	14·47	14·32	13·61	2·66	2·68
Phosphoric acid	38·72	38·89	38·80	37·44	37·24	37·83	37·50	39·44	32·86	29·92	31·15	28·00	34·08	34·12	34·10	38·04	38·07	38·05	34·09	40·97	40·35
Sulphuric acid	1·18	1·18	1·18	1·23	1·22	1·16	1·22	1·54	2·23	2·56	2·61	2·84	1·76	1·77	1·76	2·52	2·33	2·43	2·71	0·36	1·13
Carbonic acid	1·25	1·00	1·13	1·72	1·74	1·74	1·73	(0·66)	(0·27)	0·62	0·45	0·90	1·71	1·81	1·76	(0·00)	(0·00)	(0·00)	0·56	0·76	1·57
Chlorine	3·74	3·79	3·77	3·36	3·36	3·03	3·25	3·01	4·47	4·73	3·89	3·15	4·64	4·63	4·64	9·75	7·65	8·80	9·90	1·24	1·31
Silica	0·30	0·31	0·31	0·39	0·33	0·46	0·40	0·43	1·40	2·14	2·10	3·16	1·25	1·24	1·29	1·20	1·02	1·11	1·10	0·14	0·16
Sand	1·20	1·09	1·14	1·44	1·93	1·40	1·61	2·10	5·76	10·93	11·61	15·64	2·73	2·78	2·75	3·60	2·77	3·68	3·62	0·29	0·45
Charcoal	Trace	Trace	Trace	Trace	Trace	Trace	Trace	None	Trace	Trace	Trace	Trace	Trace	Trace	Trace	0·27	0·41	1·78	Trace	Trace
Total	100·86	100·87	100·87	100·73	100·76	100·69	100·72	100·67	101·02	101·06	100·68	100·72	101·05	101·05	101·05	102·21	101·78	102·00	102·66	100·28	100·30
Deduct O=Cl	0·86	0·87	0·87	0·72	0·76	0·69	0·72	0·67	1·02	1·06	0·68	0·72	1·05	1·05	1·05	2·21	1·78	2·00	2·66	0·28	0·30
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
3. COMPOSITION OF PURE ASH (THAT IS, EXCLUDING SAND AND CHARCOAL), CALCULATED TO 100.																					
Iron peroxide	1·15	1·05	1·10	1·12	1·52	1·31	1·32	1·78	2·41	2·68	2·73	4·87	2·13	2·06	2·09	4·41	4·84	4·62	6·05	0·20	0·28
Lime	41·29	41·49	41·39	44·75	44·18	44·60	44·51	41·16	35·91	36·42	37·35	35·22	36·97	36·97	36·97	2·53	2·52	2·56	3·87	49·76	49·41
Magnesia	1·70	1·67	1·68	1·58	1·65	1·94	1·72	1·32	1·67	1·77	1·57	1·81	1·70	1·69	1·69	1·70	2·62	2·16	1·40	1·17	1·03
Potash	6·42	6·51	6·46	5·92	5·17	5·12	5·40	4·80	7·16	7·27	7·37	7·89	8·22	8·25	8·23	24·04	24·46	24·25	25·52	1·66	1·68
Soda	6·66	6·50	6·58	5·40	5·51	5·77	5·56	6·41	6·91	6·99	6·56	6·03	7·29	7·29	7·29	14·76	15·07	14·92	14·43	2·66	2·70
Phosphoric acid	39·20	39·32	39·26	38·00	37·97	38·36	38·12	39·27	34·46	33·60	33·54	32·15	35·04	35·10	35·07	39·67	39·67	39·67	36·75	41·06	40·58
Sulphuric acid	1·19	1·19	1·19	1·26	1·24	1·17	1·23	1·56	2·42	2·87	2·17	3·26	1·81	1·82	1·82	2·63	2·43	2·53	2·87	0·36	1·11
Carbonic acid	1·26	1·01	1·14	1·75	1·77	1·76	1·76	0·90	0·39	0·92	0·99	1·07	1·75	1·86	1·81	(0·00)	(0·00)	(0·00)	0·28	0·76	1·58
Chlorine	3·78	3·83	3·80	3·41	3·42	3·06	3·30	3·07	4·74	5·31	3·98	3·72	4·77	4·76	4·76	10·17	8·18	9·18	10·49	1·25	1·32
Silica	0·30	0·31	0·31	0·40	0·34	0·47	0·41	0·43	1·48	2·40	2·26	3·72	1·29	1·28	1·34	1·26	1·06	1·16	1·17	0·14	0·16
Total	100·85	100·86	100·86	100·72	100·77	100·70	100·73	100·69	101·07	101·21	100·76	100·84	101·07	101·07	101·07	102·29	101·85	102·07	102·82	100·28	100·30
Deduct O=Cl	0·85	0·86	0·86	0·72	0·77	0·70	0·73	0·69	1·07	1·21	0·76	0·84	1·07	1·07	1·07	2·29	1·85	2·07	2·82	0·28	0·30
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00

APPENDIX-TABLE III.—Percentage Composition of the Ash of the Entire Bodies (excluding Contents of Stomachs and Intestines) of Ten Animals.

	Fat Calf.	Half-fat Ox.	Fat Ox.	Fat Lamb.	Store Sheep.	Half-fat old sheep.	Fat Sheep. Analysis 1.	Fat Sheep. Analysis 2.	Fat Sheep. Mean.	Very fat Sheep.*	Store Pig.	Fat Pig.
1. ACTUAL ANALYSES OF CRUDE ASH.												
Iron peroxide	0·32	0·26	0·41	0·33	1·20	1·32	0·70	1·22	0·96	0·13	0·91	0·77
Lime	42·40	44·05	46·08	43·26	41·90	43·29	42·78	42·75	42·75	53·25	40·43	38·68
Magnesia	2·17	2·01	1·51	1·79	1·77	1·68	1·68	1·77	1·72	1·75	2·00	2·05
Potash	5·33	4·37	4·41	5·65	5·48	5·14	5·30	5·29	5·30	0·37	7·36	8·01
Soda	3·77	3·05	3·00	2·82	2·79	3·27	3·36	3·45	3·41	1·72	4·14	4·39
Phosphoric acid	39·86	39·86	39·33	38·34	37·86	38·18	37·21	37·09	37·11	40·88	39·97	40·34
Sulphuric acid	1·07	0·85	0·76	1·16	1·73	1·03	0·84	0·99	0·97	0·82	2·32	2·16
Carbonic acid	1·32	1·95	2·11	1·51	1·06	1·78	(1·29)	1·61	1·61	2·04	0·60	1·21
Chlorine	1·53	1·23	1·45	1·83	2·24	1·57	1·53	1·54	1·54	0·22	2·21	2·79
Silica	0·12	0·24	0·08	0·32	0·65	0·61	0·81	0·83	0·82	0·04	0·18	0·14
Sand	0·79	1·11	0·99	1·53	2·25	2·32	2·93	4·27	4·10	0·51	0·66	0·79
Charcoal	Trace	Trace	Trace	None	Trace	None	Trace	None	Trace	Trace	Trace	Trace
Total	99·83	100·43	100·03	100·34	100·93	101·19	99·46	100·81	100·29	101·23	100·78	101·92
Deduct O=Cl	0·35	0·28	0·33	0·41	0·51	0·35	0·34	0·35	0·35	0·05	0·50	0·63
Total	99·53	100·20	99·72	99·93	100·42	100·84	99·14	100·46	99·94	101·18	100·28	101·29
2. COMPOSITION OF CRUDE ASH, CALCULATED TO EXACTLY 100.												
Iron peroxide	0·32	0·26	0·41	0·33	1·19	1·31	0·71	1·21	0·96	0·13	0·91	0·78
Lime	42·60	44·75	46·21	43·39	41·73	42·98	42·12	42·35	42·78	52·63	40·32	38·19
Magnesia	2·18	2·00	1·52	1·79	1·76	1·66	1·67	1·76	1·72	1·73	1·99	2·02
Potash	5·36	4·36	4·42	5·66	5·46	5·10	5·35	5·27	5·31	0·37	7·34	7·90
Soda	3·79	3·04	3·01	2·82	2·77	3·24	3·39	3·44	3·41	1·70	4·13	4·32
Phosphoric acid	40·04	39·78	39·44	38·37	37·70	37·86	37·53	36·92	37·14	40·40	39·86	39·83
Sulphuric acid	1·07	0·85	0·76	1·16	1·72	1·02	0·85	0·99	0·97	0·82	2·31	2·13
Carbonic acid	1·33	1·95	2·12	1·51	1·06	1·77	(1·30)	1·60	1·60	2·01	0·60	1·20
Chlorine	1·54	1·23	1·45	1·83	2·23	1·56	1·54	1·53	1·54	0·22	2·20	2·76
Silica	0·12	0·24	0·08	0·32	0·65	0·61	0·82	0·83	0·82	0·04	0·18	0·14
Sand	0·80	1·11	0·99	1·53	2·24	2·29	2·96	4·25	4·10	0·50	0·66	0·78
Charcoal	Trace	Trace	Trace	None	Trace	None	Trace	None	Trace	Trace	Trace	Trace
Total	100·35	100·28	100·33	100·41	100·51	100·35	100·24	100·35	100·35	100·05	100·50	100·63
Deduct O=Cl	0·35	0·28	0·33	0·41	0·51	0·35	0·34	0·35	0·35	0·05	0·50	0·63
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00
3. COMPOSITION OF PURE ASH (THAT IS, EXCLUDING SAND AND CHARCOAL), CALCULATED TO 100.												
Iron peroxide	0·53	0·97	0·41	0·84	1·24	1·35	0·74	1·27	1·00	0·13	0·91	0·76
Lime	43·36	45·26	46·62	44·57	43·13	44·39	44·00	44·44	44·21	52·89	40·56	39·49
Magnesia	2·20	2·03	1·52	1·82	1·82	1·72	1·74	1·84	1·79	1·74	2·01	2·04
Potash	5·40	4·41	4·46	5·74	5·64	5·27	5·57	5·50	5·53	0·37	7·39	8·57
Soda	3·82	3·08	3·04	2·86	2·86	3·35	3·53	3·59	3·56	1·71	4·16	4·46
Phosphoric acid	40·37	40·22	39·80	38·96	38·96	39·15	39·08	38·54	38·72	40·61	40·12	40·14
Sulphuric acid	1·08	0·86	0·79	1·18	1·78	1·06	0·90	1·03	1·01	0·82	2·33	2·15
Carbonic acid	1·34	1·97	2·13	1·53	1·09	1·83	(1·35)	1·67	1·67	2·02	0·60	1·20
Chlorine	1·55	1·24	1·47	1·86	2·31	1·61	1·61	1·60	1·61	0·22	2·22	2·78
Silica	0·12	0·24	0·08	0·33	0·67	0·63	0·85	0·86	0·86	0·04	0·18	0·14
Total	100·36	100·28	100·33	100·41	100·53	100·36	100·36	100·58	100·36	100·05	100·50	100·63
Deduct O=Cl	0·36	0·28	0·33	0·41	0·53	0·36	0·36	0·36	0·36	0·05	0·50	0·63
Total	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00	100·00

* There has doubtless been some omission of parts in making the mixture for burning to ash in this case, see p. 874.

APPENDIX-TABLE IV.—Mineral Constituents (Ash), in lbs., *per Animal*, and *per* 1,000 *lbs. Fasted Live-Weight.*

1. In Collective Carcass Parts. 2. In Collective Offal Parts. 3. In Entire Animal.

Entire Animal—first by addition of amounts in Carcass and Offal, second by direct analysis, third mean.

In "Offal Parts," and in "Entire Animal," in each case exclusive of contents of stomachs and intestines.

CALF AND OXEN.

	Fat Calf.					Half-fat Ox.					Fat Ox.				
	Carcass.	Offal.	Entire animal. By addition.	Entire animal. By direct analysis.	Entire animal. Mean.	Carcass.	Offal.	Entire animal. By addition.	Entire animal. By direct analysis.	Entire animal. Mean.	Carcass.	Offal.	Entire animal. By addition.	Entire animal. By direct analysis.	Entire animal. Mean.
1. "FRESH-WEIGHTS," AND CONSTITUENTS, PER ANIMAL. FRESH-WEIGHTS OF CARCASS AND OFFAL=SUM OF PARTS; ENTIRE ANIMAL=FASTED LIVE-WEIGHT.															
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weight	160·6	77·1		238·9		797·7	322·8		1232·0		839·4	376·0		1419·0	
Pure ash	7·173	2·604	9·777	9·783	9·765	42·945	12·969	56·814	56·922	56·818	42·531	12·522	55·053	55·135	55·094
Iron peroxide	0·027	0·029	0·056	0·051	0·054	0·275	0·170	0·445	0·552	0·499	0·240	0·228	0·463	0·278	0·348
Lime	3·151	1·077	4·228	4·287	4·257	20·606	5·728	26·334	25·719	26·026	19·998	5·153	25·151	25·706	25·428
Magnesia	0·190	0·044	0·194	0·214	0·204	0·784	0·189	0·937	1·149	1·043	0·734	0·161	0·895	0·946	0·920
Potash	0·413	0·116	0·529	0·527	0·533	2·139	0·599	2·538	2·505	2·521	1·932	0·601	2·533	2·459	2·496
Soda	0·231	0·170	0·391	0·373	0·382	1·141	0·715	1·656	1·747	1·702	1·105	0·902	1·907	1·674	1·790
Phosphoric acid	2·990	1·022	4·002	3·937	3·969	17·574	4·905	22·479	22·856	22·668	17·174	4·916	22·090	21·941	22·015
Sulphuric acid	0·074	0·031	0·105	0·106	0·106	0·288	0·160	0·448	0·488	0·471	0·296	0·200	0·496	0·434	0·465
Carbonic acid	0·062	0·030	0·112	0·131	0·122	0·790	0·226	1·016	1·120	1·068	0·715	0·113	0·828	1·179	1·004
Chlorine	0·073	0·099	0·172	0·151	0·162	0·328	0·425	0·753	0·707	0·730	0·373	0·385	0·758	0·807	0·782
Silica	0·008	0·008	0·016	0·012	0·014	0·120	0·052	0·172	0·138	0·156	0·060	0·054	0·114	0·045	0·080
Total	7·189	2·626	9·815	9·788	9·802	44·020	12·963	56·983	56·983	56·983	42·617	12·608	55·225	55·319	55·272
Deduct O=Cl	0·016	0·022	0·038	0·035	0·037	0·075	0·094	0·169	0·161	0·165	0·086	0·086	0·172	0·184	0·178
Total	7·173	2·604	9·777	9·753	9·765	43·945	12·869	56·814	56·822	56·818	42·531	12·522	55·053	55·135	55·094
2. "FRESH-WEIGHTS," AND CONSTITUENTS, PER 1,000 LBS. FASTED LIVE-WEIGHT. "FRESH-WEIGHTS"—EXCLUDING EVAPORATION, AND CONTENTS OF STOMACHS AND INTESTINES.															
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weight	621	296		919		647	262		909		602	265		927	
Pure ash	27·742	10·063	37·805	37·712	37·759	35·043	10·447	46·090	46·098	46·094	29·973	8·824	38·797	38·854	38·826
Iron peroxide	0·104	0·112	0·216	0·197	0·207	0·223	0·138	0·361	0·448	0·405	0·169	0·157	0·326	0·161	0·244
Lime	12·187	4·162	16·349	16·577	16·463	16·713	4·650	21·363	20·865	21·114	14·093	3·631	17·724	18·115	17·919
Magnesia	0·740	0·170	0·750	0·827	0·788	0·611	0·148	0·759	0·932	0·846	0·517	0·114	0·631	0·666	0·651
Potash	1·636	0·446	2·084	2·038	2·061	1·735	0·524	2·259	2·032	2·045	1·361	0·424	1·785	1·733	1·759
Soda	0·855	0·557	1·512	1·442	1·477	0·925	0·580	1·505	1·417	1·461	0·779	0·565	1·344	1·179	1·261
Phosphoric acid	11·526	3·949	15·475	15·223	15·349	14·254	3·982	18·236	18·644	18·390	12·103	3·464	15·567	15·462	15·514
Sulphuric acid	0·286	0·120	0·406	0·406	0·406	0·236	0·132	0·368	0·396	0·382	0·208	0·141	0·349	0·306	0·328
Carbonic acid	0·317	0·116	0·433	0·507	0·470	0·641	0·184	0·825	0·909	0·867	0·504	0·080	0·584	0·831	0·708
Chlorine	0·282	0·363	0·645	0·584	0·625	0·266	0·345	0·611	0·574	0·592	0·263	0·271	0·534	0·569	0·552
Silica	0·031	0·031	0·062	0·046	0·054	0·098	0·042	0·140	0·112	0·126	0·042	0·038	0·080	0·032	0·056
Total	27·804	10·148	37·952	37·947	37·900	35·704	10·523	46·227	46·229	46·228	30·034	8·885	38·919	38·994	38·956
Deduct O=Cl	0·062	0·085	0·147	0·135	0·141	0·061	0·076	0·137	0·131	0·134	0·061	0·061	0·122	0·130	0·126
Total	27·742	10·063	37·805	37·712	37·759	35·643	10·447	46·090	46·098	46·094	29·973	8·824	38·797	38·854	38·826

APPENDIX-TABLE V.—Mineral Constituents (Ash), in lbs., *per Animal*, and *per* 1,000 *lbs. Fasted Live-Weight.*

1. In Collective Carcass Parts. 2. In Collective Offal Parts. 3. In Entire Animal.

Entire Animal—first by addition of amounts in Carcass and Offal, second by direct analysis, third mean.

In "Offal Parts," and in "Entire Animal," in each case exclusive of contents of stomachs and intestines.

LAMB AND SHEEP.

	Fat Lamb.					Store Sheep.					Half-fat old Sheep.					Fat Sheep.					Very fat Sheep.				
	Carcass.	Offal.	Entire animal.			Carcass.	Offal.	Entire animal.			Carcass.	Offal.	Entire animal.			Carcass.	Offal.	Entire animal.			Carcass.	Offal.	Entire animal.		
			By addition.	By direct analysis.	Mean.			By addition.	By direct analysis.	Mean.			By addition.	By direct analysis.	Mean.			By addition.	By direct analysis.	Mean.			By addition.	By direct analysis.	Mean.
1. "FRESH-WEIGHTS," AND CONSTITUENTS, PER ANIMAL. WEIGHTS OF CARCASS AND OFFAL=SUMS OF PARTS; ENTIRE ANIMAL=FASTED LIVE-WEIGHT.																									
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weights	50·5	20·3		84·4		52·1	37·4		97·6		56·2	37·1		105·1		73·1	45·4		127·2		159·8	80·1		239·4	
Pure ash	1·631	0·603	2·434	2·442	2·438	2·262	0·730	2·992	2·990	2·991	2·319	0·891	3·210	3·224	3·217	2·505	0·890	3·395	3·427	3·411	4·309	2·839	7·238	7·238	7·238
Iron peroxide	0·008	0·018	0·023	0·021	0·022	0·008	0·027	0·035	0·037	0·036	0·011	0·033	0·044	0·044	0·044	0·010	0·043	0·053	0·054	0·054	0·017	0·099	0·076	(0·076)	0·076
Lime	0·857	0·217	1·074	1·069	1·072	1·027	0·266	1·293	1·240	1·267	1·021	0·333	1·404	1·462	1·433	1·169	0·313	1·482	1·529	1·505	2·063	1·050	3·133	(3·133)	3·133
Magnesia	0·032	0·010	0·043	0·044	0·044	0·042	0·013	0·055	0·054	0·055	0·041	0·014	0·056	0·055	0·056	0·045	0·016	0·061	0·062	0·061	0·090	0·049	0·138	(0·138)	0·138
Potash	0·385	0·056	0·141	0·140	0·141	0·117	0·053	0·170	0·169	0·170	0·147	0·066	0·183	0·170	0·177	0·117	0·070	0·187	0·190	0·189	0·166	0·234	0·400	(0·400)	0·400
Soda	0·045	0·042	0·087	0·087	0·087	0·067	0·051	0·118	0·116	0·117	0·061	0·050	0·111	0·106	0·110	0·070	0·054	0·124	0·122	0·123	0·120	0·207	0·327	(0·327)	0·327
Phosphoric acid	0·739	0·210	0·949	0·952	0·950	0·913	0·244	1·157	1·165	1·161	0·942	0·314	1·256	1·262	1·259	1·023	0·295	1·318	1·327	1·323	1·804	0·996	2·800	(2·800)	2·800
Sulphuric acid	0·015	0·021	0·036	0·029	0·032	0·028	0·021	0·049	0·053	0·051	0·012	0·028	0·040	0·034	0·037	0·018	0·030	0·048	0·035	0·039	0·021	0·051	0·072	(0·072)	0·072
Carbonic acid	0·033	0·002	0·035	0·037	0·036	0·032	0·007	0·039	0·033	0·036	0·043	0·009	0·052	0·059	0·055	0·037	0·010	0·047	0·057	0·052	0·073	0·051	0·123	(0·123)	0·123
Chlorine	0·017	0·028	0·045	0·045	0·045	0·033	0·038	0·072	0·069	0·070	0·024	0·030	0·054	0·058	0·056	0·028	0·033	0·056	0·056	0·056	0·081	0·185	0·266	(0·166)	0·166
Silica	0·008	0·009	0·017	0·008	0·010	0·002	0·018	0·020	0·020	0·020	0·002	0·021	0·023	0·020	0·021	0·008	0·033	0·036	0·029	0·033	0·002	0·038	0·040	(0·040)	0·040
Total	1·835	0·610	2·445	2·452	2·449	2·269	0·739	3·008	3·005	3·007	2·324	0·896	3·222	3·236	3·229	2·510	0·937	3·407	3·440	3·424	4·406	2·969	7·375	(7·375)	7·375
Ded. ots O=Cl	·004	·007	·011	·010	·0011	·007	·009	·016	·015	·0156	·005	·007	·012	·012	·0122	·005	·007	·012	·013	·0123	·007	·030	·037	(0·037)	0·037
Total	1·831	0·603	2·434	2·442	2·438	2·262	0·730	2·992	2·990	2·991	2·319	0·891	3·210	3·224	3·217	2·505	0·890	3·395	3·427	3·411	4·399	2·939	7·338	(7·338)	7·338
2. "FRESH-WEIGHTS," AND CONSTITUENTS, PER 1,000 LBS. FASTED LIVE-WEIGHT. "FRESH-WEIGHTS"—EXCLUDING EVAPORATION, AND CONTENTS OF STOMACHS AND INTESTINES.																									
	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weights	598	312		910		533	383		916		536	353		889		575	357		932		630	317		947	
Pure ash	21·682	7·145	28·827	28·924	28·876	23·158	7·469	30·627	30·603	30·615	22·094	8·476	30·570	30·697	30·634	19·715	6·998	26·713	26·960	26·836	17·402	11·234	28·636	28·636	28·636
Iron peroxide	0·095	0·177	0·272	0·249	0·261	0·082	0·276	0·358	0·379	0·369	0·105	0·314	0·419	0·419	0·419	0·079	0·338	0·417	0·288	0·343	0·067	0·234	0·301	(0·301)	0·301
Lime	10·146	2·571	12·719	12·667	12·693	10·514	2·725	13·238	12·698	12·968	10·204	3·168	13·372	13·834	13·603	9·200	2·461	11·661	12·028	11·844	8·240	4·155	12·395	(12·395)	12·395
Magnesia	0·381	0·118	0·509	0·521	0·515	0·430	0·133	0·563	0·553	0·558	0·391	0·133	0·524	0·524	0·524	0·354	0·126	0·480	0·488	0·484	0·356	0·190	0·546	(0·546)	0·546
Potash	1·906	0·664	1·670	1·656	1·664	1·198	0·542	1·740	1·730	1·735	1·405	0·625	1·743	1·619	1·681	0·921	0·550	1·471	1·495	1·483	0·656	0·926	1·582	(1·582)	1·582
Soda	0·533	0·498	1·031	1·030	1·030	0·686	0·522	1·208	1·187	1·197	0·581	0·476	1·057	1·026	1·043	0·551	0·425	0·976	0·960	0·968	0·475	0·819	1·294	(1·294)	1·294
Phosphoric acid	8·751	2·468	11·220	11·276	11·257	9·347	2·496	11·843	11·924	11·883	8·974	2·987	11·961	12·016	11·988	8·051	2·319	10·370	10·439	10·404	7·136	3·941	11·077	(11·077)	11·077
Sulphuric acid	0·178	0·248	0·427	0·344	0·386	0·287	0·215	0·502	0·543	0·522	0·114	0·266	0·380	0·324	0·352	0·101	0·236	0·338	0·275	0·307	0·083	0·202	0·285	(0·285)	0·285
Carbonic acid	0·391	0·024	0·415	0·439	0·427	0·328	0·072	0·400	0·338	0·369	0·410	0·086	0·496	0·562	0·529	0·291	0·079	0·370	0·446	0·408	0·285	0·202	0·487	(0·487)	0·487
Chlorine	0·201	0·325	0·526	0·543	0·534	0·339	0·389	0·737	0·706	0·722	0·229	0·286	0·514	0·496	0·505	0·161	0·259	0·440	0·433	0·437	0·323	0·584	0·657	(0·657)	0·657
Silica	0·095	0·107	0·142	0·095	0·119	0·020	0·184	0·204	0·205	0·205	0·019	0·200	0·219	0·190	0·204	0·024	0·259	0·283	0·228	0·255	0·008	0·150	0·158	(0·158)	0·158
Total	21·729	7·226	28·957	28·942	28·900	23·230	7·561	30·791	30·767	30·774	22·142	8·543	30·685	30·811	30·748	19·754	7·062	26·806	27·062	26·934	17·429	11·353	28·782	(28·782)	28·782
Deduct O=Cl	·047	·063	·130	·118	·0124	·072	·092	·164	·154	·0159	·046	·067	·113	·114	·0114	·039	·064	·093	·102	·0098	·027	·119	·146	(·146)	0·146
Total	21·682	7·145	28·827	28·924	28·876	23·158	7·469	30·627	30·603	30·615	22·094	8·476	30·570	30·697	30·634	19·715	6·998	26·713	26·960	26·836	17·402	11·234	28·636	(28·636)	28·636

APPENDIX-TABLE VI.—Mineral Constituents (Ash), in lbs., *per Animal*, and *per* 1,000 *lbs. Fasted Live-Weight.*
1. In Collective Carcass Parts. 2. In Collective Offal Parts. 3. In Entire Animal.
Entire Animal—first by addition of amounts in Carcass and Offal, second by direct analysis, third mean.
In "Offal Parts" and in "Entire Animal," in each case exclusive of contents of stomachs and intestines.

PIGS.

	Store Pig.						Fat Pig.					
	Carcass.	Offal, excluding Head and Feet.	Head and Feet.	Entire Animal. By Addition.	Entire Animal. By direct Analysis.	Entire Animal. Mean.	Carcass.	Offal, excluding Head and Feet.	Head and Feet.	Entire Animal. By Addition.	Entire Animal. By direct Analysis.	Entire Animal. Mean.
1. "FRESH-WEIGHTS," AND CONSTITUENTS, PER ANIMAL. WEIGHTS OF CARCASS AND OFFAL=SUM OF PARTS; ENTIRE ANIMAL=FASTED LIVE-WEIGHT.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weights	62·4	20·3	9·3		92·0		140·6	23·2	18·4		182·0	
Pure ash	1·596	0·196	0·737	2·491	2·491	2·491	1·949	0·196	0·871	3·019	3·025	3·022
Iron peroxide	0·010	0·007	0·001	0·018	0·023	0·021	0·012	0·012	0·002	0·026	0·023	0·025
Lime	0·645	0·006	0·287	1·018	1·011	1·014	0·752	0·008	0·431	1·191	1·164	1·177
Magnesia	0·084	0·003	0·013	0·060	0·060	0·060	0·041	0·003	0·014	0·058	0·062	0·060
Potash	0·135	0·026	0·012	0·165	0·184	0·188	0·189	0·050	0·014	0·253	0·259	0·256
Soda	0·060	0·023	0·020	0·103	0·104	0·104	0·085	0·028	0·024	0·137	0·132	0·135
Phosphoric acid	0·640	0·062	0·303	1·005	0·999	1·002	0·783	0·073	0·358	1·209	1·214	1·211
Sulphuric acid	0·081	0·004	0·027	0·043	0·056	0·050	0·025	0·006	0·010	0·041	0·066	0·054
Carbonic acid	0·019	0·000	0·006	0·025	0·015	0·020	0·025	0·001	0·014	0·040	0·037	0·039
Chlorine	0·029	0·014	0·009	0·052	0·055	0·053	0·044	0·021	0·011	0·076	0·084	0·080
Silica	0·002	0·002	0·001	0·005	0·005	0·005	0·003	0·002	0·001	0·006	0·004	0·005
Total	1·606	0·146	0·720	2·503	2·504	2·504	1·959	0·204	0·874	3·037	3·044	3·041
Deduct O=Cl.	0·007	0·008	0·002	0·012	0·013	0·013	0·010	0·008	0·003	0·019	0·019	0·019
Total	1·596	0·156	0·737	2·491	2·491	2·491	1·949	0·196	0·871	3·018	3·025	3·022
2. "FRESH-WEIGHTS," AND CONSTITUENTS, PER 1,000 LBS. FASTED LIVE-WEIGHT. "FRESH-WEIGHTS"—EXCLUDING EVAPORATION, AND CONTENTS OF STOMACHS AND INTESTINES.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.	lbs.
Fresh-weights	664	216	98		978		760	125	72		957	
Pure ash	17·068	1·953	7·825	26·491	26·512	26·501	10·539	1·068	4·686	16·295	16·346	16·320
Iron peroxide	0·106	0·078	0·011	0·192	0·248	0·218	0·065	0·065	0·011	0·141	0·124	0·133
Lime	6·863	0·064	3·046	10·823	10·761	10·792	4·066	0·043	2·320	6·429	6·290	6·359
Magnesia	0·892	0·032	0·138	0·632	0·642	0·638	0·223	0·016	0·075	0·313	0·336	0·324
Potash	1·440	0·268	0·127	1·755	1·954	1·963	1·022	0·269	0·075	1·366	1·400	1·380
Soda	0·638	0·245	0·212	1·095	1·107	1·101	0·460	0·151	0·129	0·740	0·713	0·727
Phosphoric acid	6·810	0·661	3·217	10·688	10·632	10·660	4·224	0·394	1·930	6·528	6·860	6·544
Sulphuric acid	0·330	0·043	0·074	0·447	0·617	0·532	0·135	0·033	0·054	0·222	0·351	0·286
Carbonic acid	0·202	0·000	0·064	0·266	0·160	0·213	0·135	0·005	0·075	0·215	0·350	0·283
Chlorine	0·309	0·149	0·096	0·554	0·585	0·570	0·238	0·113	0·059	0·410	0·454	0·432
Silica	0·021	0·021	0·011	0·053	0·053	0·053	0·016	0·011	0·006	0·033	0·022	0·028
Total	17·027	1·695	7·846	26·619	26·650	26·634	10·593	1·100	4·704	16·397	16·449	16·423
Deduct O=Cl.	0·024	0·032	0·021	0·127	0·138	0·133	0·054	0·032	0·016	0·102	0·103	0·103
Total	17·003	1·663	7·825	26·491	26·512	26·501	10·539	1·068	4·688	16·295	16·346	16·320

XXVII. The Bakerian Lecture.—*On Radiant Matter Spectroscopy: The Detection and wide Distribution of Yttrium.*

By William Crookes, *F.R.S.*

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Introduction.

1. In March, 1881, I sent to the Royal Society a preliminary notice of some results I had obtained when working on the molecular discharge in high vacua.* When the spark from a good induction coil traverses a tube having a flat aluminium pole at each end, the appearance changes according to the degree of exhaustion. Supposing atmospheric air to be the gas under exhaustion, at a pressure of about 7 millims. a narrow black space is seen to separate the luminous glow and the aluminium pole connected with the negative pole of the induction coil. As the exhaustion proceeds this dark space increases in thickness, until, at a pressure of about 0·02 millim. (between 20 and 30 M.)†, the dark space has swollen out till it nearly fills the tube. The luminous cloud showing the presence of residual gas has almost disappeared, and the molecular discharge from the negative pole begins to excite phosphorescence on the glass where it strikes the side. There is great difference in the degree of exhaustion at which various substances begin to phosphoresce. Some refuse to glow until the exhaustion is so great that the vacuum is nearly non-conducting, whilst others begin to become luminous when the gauge is 5 or 10 millims. below the barometric level. The majority of bodies, however, do not phosphoresce till they are well within the negative dark space. This phosphorogenic phenomenon is at its maximum at about 1 M., and, unless otherwise stated, the experiments now about to be described were all tried at this high degree of exhaustion.

Under the influence of this discharge, which I have ventured to call radiant matter, a large number of substances emit phosphorescent light, some faintly and others with great intensity. On examining the emitted light in the spectroscope most bodies give a faint continuous spectrum, with a more or less decided concentration in one part of the spectrum, the superficial colour of the phosphorescing substance being governed by this preponderating emission in one or other part of the spectrum.

Sometimes, but more rarely, the spectrum of the phosphorescent light is discontinuous, and it is to bodies manifesting this phenomenon that my attention has been

* Proceedings of the Royal Society, No. 213, 1881.

† M. = one-millionth of an atmosphere.

specially directed for some years past, considerable interest attaching to a solid body whose molecules vibrate in a few directions only, giving rise to spectrum lines or bands on a dark background.

The citron band spectrum.

2. For a long time past I have been haunted by a bright citron-coloured band or line appearing in these phosphorescent spectra, sometimes as a sharp line, at others as a broader nebulous band, but having always a characteristic appearance and occurring uniformly in the same spot. This band I first saw in the summer of 1879, and from that date down to a comparatively short time ago all my efforts to clear up the mystery proved vain. By chemical means it was not difficult to effect a partial separation of a certain mineral or earthy body into two parts, one giving little or no citron band, the other giving one stronger than the original band; and by again treating this latter portion by appropriate chemical means, the citron band-forming body could frequently be still more concentrated; but further than this for a long time it seemed impossible to go. I soon came to the conclusion that the substance I was in search of was an earth, but on attempting to determine its chemical properties I was baffled. A more Proteus-like substance a chemist never had to deal with. In my preliminary note, above referred to, speaking of the possibility that some of these spectrum-forming bodies might be new chemical elements, I said—"The chemist must be on his guard against certain pitfalls which catch the unwary. I allude to the profound modification which the presence of fluorine, phosphorus, boron, &c., causes in the chemical reactions of many elements, and to the interfering action of a large quantity of one body on the chemical properties of another which may be present in small quantities."

3. This warning was not unnecessary. No Will-o'-the-Wisp ever led the unwary traveller into so many pitfalls and sloughs of despond as the hunt for this phantom band has entrapped me. I have started with a large quantity of substance which, from preliminary observations, promised to be a rich mine of the desired body, and have worked it up chemically to a certain point, when the citron band vanished, and could not be again detected in either precipitate or filtrate. Half-a-dozen times in the last four years the research has been given up as hopeless, and only a feeling of humiliation at the thought of a chemist being beaten by any number of anomalies made me renew each time the attack. Likewise, the tedious character of the research made a long continuance of failures very disheartening. To perform a spectrum test, the body under examination must be put in a tube and exhausted to a very high point before the spectroscope can be brought to bear on it. Instead of a few minutes, many hours are occupied in each operation, and the tentative gropings in the dark, pre-eminently characteristic of this kind of research, have to be extended over a long period of time.

4. I soon found that the best way to bring out the band was to treat the substance

under examination with strong sulphuric acid, drive off excess of acid by heat, and finally to raise the temperature to dull redness (10). The anhydrous sulphate thus left frequently showed the citron band in the radiant matter tube, when before this treatment the original substance showed nothing (75).

Examination of calcium compounds.

5. My first idea was that the band might be due to a compound of lime. Much chemical evidence tended to support this view. I have already explained that the chemical extraction was rendered very difficult by the fact of the citron band so frequently turning up both in the precipitate and the filtrate. By neglecting the portion showing least citron band, and separating all the elements present which gave little or none, I could generally concentrate the citron band into a solution which —according to our present knowledge of analytical chemistry—should contain little else than the earths, alkaline earths, and alkalies. Ammonia added to this solution would precipitate an earth (11, 14), and in the filtrate oxalic acid would precipitate an insoluble oxalate (7, 13).

The citron band hovered between these two precipitates, being sometimes stronger in one and sometimes in the other. It was also to be detected, but more faintly, in the residue left after evaporating to dryness and igniting the filtrate from the oxalate.

I frequently obtained no precipitate with ammonia, and then the oxalate gave the band brilliantly; and occasionally the ammonia precipitate when formed gave little or no citron band. I was, however, generally sure to find it in the insoluble oxalate, and sometimes it was very brilliant, being accompanied by two bright green bands and a fainter red band.

6. At this time one of the minerals which showed the citron band most strongly was a phosphorescent apatite from Ireland; and knowing the difficulties of separating the last traces of phosphoric acid from the earths, I explained the foregoing facts by the presence of small quantities of phosphoric acid, which gave rise to the ammonia precipitate; the bulk of the citron body not being precipitated by ammonia, but coming down as oxalate; whilst a little of this oxalate would remain dissolved in the ammoniacal salts present, and so appear with the alkalies.

I tested this hypothesis in every imaginable way, by mixing small quantities of phosphoric acid with salts of lime and other earths, in the endeavour to imitate the conditions occurring in the native minerals, and so educe the citron band; but I was unable to get any precipitate giving the citron band when I started with materials which did not originally give it.

7. A sufficient quantity of precipitated oxalate (5) having in course of time been accumulated, I attempted its purification. It was ignited, dissolved in dilute hydrochloric acid, and rendered slightly alkaline with ammonia and ammonic sulphide. The liquid was boiled to a small bulk, keeping it alkaline, and was then set aside in

a warm place: a slight flocculent precipitate formed. This was filtered, and the filtrate re-concentrated. The clear strong solution should now contain nothing but barium, strontium, and calcium, with traces of elements from previous groups which might be soluble in the precipitants employed or in the ammoniacal salts present (for we know that the word *insoluble* applied to a precipitate is not an absolute term, and in minute analysis allowance must be made not only for the slight solubility of precipitates in the reagents present, but also for the power possessed by most precipitates of carrying down with them traces of soluble metallic salts from solution). Besides these, it was possible that a hitherto unrecognised element might be present, to which the citron band was due. By the ordinary process of analysis I could, however, only detect the presence of calcium and strontium.

8. The concentrated ammoniacal solution was added to an excess of a boiling solution of ammonic sulphate, and the whole was set aside for twenty-four hours; the precipitate which had formed was filtered off and washed with a saturated solution of ammonic sulphate. The precipitate was found to consist of strontic sulphate. On testing this in a radiant matter tube the citron band was very decided, although much fainter than in the original oxalate. The filtrate was diluted largely, heated, and precipitated with a hot solution of ammonic oxalate; it was then allowed to stand for some time, when a bulky white calcic oxalate came down. This was filtered and washed. Tested in the radiant matter tube, after ignition and treatment with sulphuric acid, it gave the citron band, far exceeding in brightness the spectrum of the original oxalate.

9. So far all the chemical evidence went to show that the band-forming substance was calcium, and further tests tried with the purified oxalate confirmed this inference. Every analytical test to which it was subjected showed lime, and nothing but lime; all the salts which were prepared from it resembled those of lime, both physically and chemically; the flame spectrum gave the calcium lines with extraordinary purity and brilliancy; and finally, the atomic weight, taken with great care, came out almost the same as that for calcium, 39·9 as against Ca 40.

10. I now sought for the citron band amongst other calcium minerals. The preliminary testing was simple. The finely powdered mineral was moistened with strong sulphuric acid, the action being assisted by heat, and the mass was then raised to dull redness (4). It was then put into a radiant matter tube and the induction spark passed through after the exhaustion had been pushed to the required degree.

Treated in this manner most native compounds of lime gave the citron band. A perfectly clear and colourless crystal of Iceland spar converted into sulphate gave it strongly, native calcic phosphate less strongly, and a crystal of arragonite much more brightly. A stalactite of calcic carbonate from the Gibraltar caves gave the band almost as well as calcite, as also did cinnamon stone (lime alumina garnet), iron slag from a blast-furnace, commercial plaster of Paris, and most specimens of ordinary burnt lime.

The citron band not due to calcium.

11. Evidence stronger than this in favour of the view that the citron band was an inherent characteristic of calcium could scarcely be; but, on the other hand, there was evidence equally conclusive that the band was not essential to calcium. The ammonia precipitate (5) sometimes gave the citron band with great strength and purity, and although I had not yet obtained this in quantities sufficient for a detailed examination, it was easy to decide that it contained no phosphoric, silicic, or boric acid, fluorine, or other body likely to cause the precipitation of lime in this group. This precipitate must therefore be an earth, and the more carefully I purified it from lime and other substances, the more brilliantly shone out the citron band, and the more intense became the green and red bands.

Another stubborn fact was this:—Starting with a lime compound which showed the citron band, I could always obtain a calcic oxalate which gave the band stronger than the original substance; but if I started with a lime compound which originally gave no citron band, I could never by any means, chemical or physical, constrain the lime or the earthy precipitate to yield a citron band.

12. Among the minerals tried was eudialyte, a silicate of zirconium, iron, calcium, and sodium, containing about 10 per cent. of lime. No citron band could be detected on testing the original mineral or any of the constituents separated from it on analysis. This, and a lump of common whiting (levigated chalk), were for some time my only sources of lime which gave no citron band.

13. The only explanation that I could see for this anomaly was that the elusive citron band was caused by some element precipitated with the calcic oxalate, but present in a quantity too small to be detected by ordinary chemical means. I then thought that were I to fractionally precipitate the solution of lime, the band-forming body might be concentrated in one or the other portion. Accordingly the calcic oxalate (7, 8, 9) was ignited and dissolved in hydrochloric acid, and fractionally precipitated in three portions with ammonic oxalate, the first and third portions being comparatively small. They were dried, ignited with sulphuric acid, and tested in the radiant matter tube. All three portions showed the citron band, but the portion which came down first gave the band decidedly the strongest, and the third portion precipitated showed it weakest. This therefore pointed to a difference between calcium and the body sought for. The process, however, was not satisfactory, and I was driven to seek some other method.

14. A portion of an ammonia precipitate found to give the citron band very well (5, 11), was dissolved in dilute sulphuric acid, and the solution evaporated down. Crystals were formed which were difficultly soluble in hot water, but appeared more soluble than calcic sulphate.

A large quantity of the calcic oxalate (7, 8, 9) was ignited with sulphuric acid at a dull red heat, and the resulting calcic sulphate was finely ground and then boiled in a

very small quantity of water—not sufficient to dissolve the one-hundredth part of it. The mass was thrown on a filter, and the small quantity of clear liquid which came through was precipitated with ammonic oxalate. The resulting white precipitate was ignited with sulphuric acid, and tested in the radiant matter tube. For the sake of comparison a portion of the calcic sulphate remaining on the filter was also put in a radiant matter tube. The sulphate from the aqueous extract gave the citron band far more brilliantly than the calcic sulphate from the filter. I found, however, that it was impossible, by any amount of washing or boiling out, to deprive the calcic sulphate of all power of giving the citron band, although it was possible in this way to weaken its intensity considerably.

Experiments with calcic sulphate.

15. Supposing that the substance giving the citron band formed a sulphate more soluble in water than calcic sulphate, it was anticipated that repeated washings with cold water would extract some of it, which might then be detected more easily. About four pounds' weight of commercial plaster of Paris, which showed very faint traces of the citron band, were mixed with water and rapidly poured on a large filter. Before the mass solidified a slight saucer-like depression was made in the upper part, and a few ounces of water were poured on. This ran through slowly, and it was then poured back and the exhaustion repeated several times. The aqueous extract was then evaporated to dryness, ignited with sulphuric acid, ground in a mortar with small successive quantities of water, the liquid boiled, filtered, and precipitated, first with ammonia, and the filtrate with ammonic oxalate. These precipitates both showed the citron band very fairly, far more intensely than it was seen in the original calcic sulphate. The green and red bands were also visible.

The same mass of plaster of Paris was then washed, as before, with a little dilute hydrochloric acid passed through several times, and this extract was treated in the same way by evaporation and extraction with water, and the filtrate precipitated, first with ammonia, and then with ammonic oxalate. In these precipitates the citron band, together with the green and red bands, were much more brightly manifest than in the precipitates from the aqueous extract.

Wide distribution of the citron band-forming body.

16. These experiments are conclusive in proving that the citron band is not due to calcium, but to some other element, probably one of the earthy metals, occurring in very minute quantities, but widely distributed along with calcium, and I at once commenced experiments to find a more abundant supply of the body sought for. Amongst other substances tested I may note the following as giving a more or less decided citron band in the spectrum when treated with sulphuric acid in the manner indicated above (10):—Crystallised barytic chlorate, heavy spar, common limestone, strontic nitrate, native strontic carbonate, crystallised uranic nitrate, commercial

magnesic sulphate, commercial potassic sulphate, Wagnerite (magnesic phosphate and fluoride), zircon, cerite, and commercial ceric oxalate.

Examination of zircon for the citron band.

17. Some specimens of zircon treated in the above manner appeared sufficiently rich to make it probable that here might be found an available source of the citron-band-yielding body. I found it in crystals from Green River, North Carolina, from Ceylon, from Expailly, from Miask (Oural), and from Brevig, and having a good supply of North Carolina zircons I started working up these in the following manner:—

The finely-powdered zircons were fused with sodic fluoride, and the melted mass powdered, boiled with sulphuric acid, and filtered. The solution was precipitated with excess of ammonia, the precipitate well washed and dissolved in hydrochloric acid, and the solution made nearly neutral. A little zirconic oxychloride sometimes separated on evaporation; this was filtered off. An excess of sodic thiosulphate was now added, and the whole boiled for some time until a portion of the filtrate gave no further precipitate on boiling again with sodic thiosulphate. The precipitated zirconic thiosulphate was worked up for zirconia; it was found to be quite free from the substance giving the citron band. The solution filtered from the zirconic thiosulphate was precipitated with ammonia, and the brown gelatinous precipitate was well washed. The filtrate was precipitated with ammonic oxalate, which brought down much calcic oxalate. This showed the citron band, but not strongly. The brown gelatinous precipitate was dissolved in nitric acid. Argentic nitrate was added to separate chlorine, and the filtrate from the argentic chloride was boiled down with nitric acid and excess of metallic tin to separate phosphoric acid. The clear solution, separated from the stannic oxide, phosphate, &c., was boiled down with hydrochloric acid to remove nitric acid, and then saturated with hydric sulphide to separate silver and tin.

18. The filtrate from the sulphides was freed from hydric sulphide by boiling, and was then mixed with tartaric acid and excess of ammonia, to precipitate any yttria that might be present, together with Forbes's zirconia β* (jargonia?). On standing for some hours this gave a small quantity of a precipitate, which was separated by filtration; it was tested in the radiant matter tube, and found not to give the citron-band spectrum (44). To the filtrate ammonic sulphide was added to precipitate the iron. The black precipitate was filtered off, and the filtrate evaporated to dryness, and ignited to destroy the organic matter. The residue, heated with sulphuric acid and ignited, gave the citron spectrum very brightly. This would probably be the earth which Forbes calls zirconia γ.†

* 'Chem. News,' vol. 19, p. 277.

† *Loc. cit.*

19. For many years chemists have suspected that what is known as zirconia might be a compound. SVANBERG* found that zircons from different localities varied in specific gravity, and the earth or earths obtained by fractional precipitation with oxalic acid had not the same properties, the hydrogen equivalents of the metals of the earths of the different fractions varying from 17·01 to 27·3, the metal of the earth hitherto recognised as zirconia being 22·4.† He considered zirconia to contain two different earths, the oxalate of one being less soluble in acid than that of the other, and their sulphates differing in crystalline form and solubility. He proposed the name "noria" for one of the earths, retaining that of zirconia for the other. The researches of BERLIN, on the other hand, seem to disprove this.

20. Remembering the remarkable result produced in the absorption spectrum of some jargons by the presence of a minute trace of uranium,‡ I tried numerous experiments with this metal, adding small quantities of it to zirconia, lime, thoria, ceria, &c., but in no case could I educe the citron-band spectrum by this means.

I may condense a year's work on zircon,—more than ten pounds weight of crystals from North Carolina having been worked up—by stating that the result was comprised in about 300 grains of an earthy residue (18), and about two ounces of oxalate, chiefly calcium; the former gave the citron band very well. The process as detailed above is given, since by this means a very large quantity of zircons was worked up, affording me the material which ultimately enabled me to solve the problem which at one time seemed almost hopeless.

The zirconia prepared from these zircons when tested sometimes showed the citron band, especially after precipitation as an oxychloride. Zirconia precipitated as thiosulphate did not yield the citron band (28). A zirconia rich in citron band, fractionally precipitated by ammonia, yielded precipitates of increasing richness, the last fraction showing the citron band strongly.

21. The calcic oxalate obtained from zircon gave unsatisfactory results, so attention was directed to the earthy residue (18). This was found to be of highly complex character, containing thoria (which had escaped precipitation as thiosulphate), ceria, lanthana, didymia, yttria, and probably some of the newly-discovered rarer earths.

Examination of cerite for the citron band.

22. The position of the citron band in the spectrum falls exactly on the strongest absorption band of didymium, so that a piece of didymium glass or cell of solution of the nitrate entirely obliterates the citron band. This naturally suggested that the band was due to didymium.

* Pog. Ann., vol. 65, p. 317.

† SVANBERG's numbers for these earths are 938 to 1320 (M_2O_3), the earth hitherto recognised as zirconia being 1140; oxygen being 100. For the sake of uniformity I have recalculated his equivalents for the metals on the O = 16 scale, taking the formula as M_2O (see note 1, par. 40).

‡ 'Chem. News,' vol. 19, pp. 121, 142, 205, 277; vol. 20, pp. 7, 104; vol. 21, p. 73.

Cerite was accordingly the next mineral experimented on. The powdered mineral tested in the tube in the original way gave a good citron band. It was made into a paste with sulphuric acid, and after all action had ceased it was extracted with cold water. The earths were then precipitated with ammonic oxalate, and the oxalate ignited. The fawn-coloured powder was then converted into sulphate, dissolved in water, and the cerium metals precipitated by long digestion with excess of potassic sulphate. When no didymium bands could be detected in a considerable thickness of the supernatant liquor it was assumed that all the cerium metals were down, and the liquid was filtered.

23. The precipitated double sulphates were dissolved in hydrochloric acid, and the earths precipitated as oxalates. After ignition and treatment with sulphuric acid, the mixed ceria, lanthana, and didymia were tested in the radiant matter tube, but the merest trace only of citron band was visible.

24. This experiment proved the inadequacy of the didymium explanation (22), and further tests showed that not only could I get no citron band in pure didymium compounds, but the spectrum entirely failed to detect didymium in many solutions of the earth which gave the citron band brilliantly.

25. Attention was now turned to the solution filtered from the insoluble double sulphates from cerite (22). Potash in excess was added to the filtrate, and the flocculent precipitate filtered off, and after well washing was converted into sulphate, and tested in a radiant matter tube. The spectrum, of extraordinary brilliancy, was far brighter than any I had hitherto obtained. Unfortunately, however, the quantity was too small to be subjected to very searching chemical analysis.

Examination of thorite and orangite.

26. Search was next made amongst other minerals rich in the rarer earths. Thorite, another disputed mineral, was finely powdered, treated with sulphuric acid, and tested in the radiant matter tube. It gave the citron spectrum most brilliantly —equal, in fact, to the mixture of earths obtained from zircons (18, 21) at so great an expenditure of time and trouble. Orangite treated in the same manner gave almost as good a spectrum. Pure thorinic sulphate prepared by myself was found not to give the citron band, but three specimens prepared and given to me by friends all gave it, so it was not unlikely that in thorite and orangite might at last be found a good source of the long-sought element—that in fact the body I was hunting for, if not thorina, might possibly be BAHR's hypothetical wasium. Having obtained about 2 lbs. of orangite and thorite, they were worked up as follows :—

27. The finely-powdered mineral was heated for some time with strong hydrochloric acid, and when fully gelatinised and all action had ceased, it was evaporated to dryness to render the silica insoluble; then extracted with water slightly acidulated with hydrochloric acid, boiled, and filtered. Hydric sulphide was passed through the

filtrate for some time. The flask then corked was set aside for twenty-four hours and filtered. The filtrate was evaporated to a small bulk, nearly neutralised with ammonia, and then boiled for some time with excess of sodic thiosulphate. This precipitated the thorina, alumina, zirconia, and titanic acid, whilst it left in solution the metals of the cerium and yttrium groups. The filtrate was boiled down to a small bulk, when a further precipitation took place: this was filtered off and added to the first thiosulphate precipitate. To the clear filtrate excess of ammonic oxalate was added, and the whole allowed to rest twenty-four hours. The precipitated oxalates were filtered, washed, ignited, dissolved in hydrochloric acid, and the excess of acid evaporated off. The aqueous solution was then mixed with a large excess of freshly precipitated baric carbonate, and set aside for twenty-four hours with frequent shaking (29). This would precipitate much of the cerium, and any iron or alumina which might have escaped previous treatment. The liquid was filtered from the precipitate produced by baric carbonate, and the clear solution, which would contain nothing but barium, and some of the yttrium and cerium metals, was treated as described further on (30).

28. The thiosulphate precipitate tested in the radiant matter tube gave no citron band, nor did it seem possible to detect this band on testing the purified thorina obtained from this precipitate, nor from the alumina or zirconia from the same precipitate. This confirmed the results obtained when working up zircons, that sodic thiosulphate did not precipitate the citron band-forming body.

29. The barium precipitate (27) was dissolved in hydrochloric acid, the baryta separated with sulphuric acid, and the solution precipitated with ammonic oxalate. The ignited precipitate, which amounted to 0·223 per cent. of the mineral taken, contained the cerium metals. On testing in a radiant matter tube it gave the citron band only moderately well—not nearly so strong as the original thorite and orangite. The iron and alumina in the filtrate from the ceric oxalates were likewise precipitated and tested; they showed a faint trace of citron band.

30. The solution (27) filtered from the barium precipitate was freed from baryta by sulphuric acid, precipitated with ammonic oxalate, and the precipitate washed and ignited; it amounted to only 0·125 of the mineral taken. Tested in the radiant matter tube it showed the citron band about as well as the corresponding earth from the barium precipitate.

This was disheartening, for after having started with a mineral which gave the citron band well, and having hunted the citron band as it were into a corner, the only result was two trifling precipitates showing the citron band less intensely than did the raw material itself. The experiment, however, proved one thing: the band-forming substance was not thorina. The occurrence of this spectrum must therefore be due to some other element present in small quantity in thorite and orangite.

31. The two mixtures of earths—the one from the barium precipitate (29) and the other from the barium filtrate (30)—which showed the citron line moderately well,

were dissolved in sulphuric acid, the solution neutralised as nearly as possible with potash, and digested for several days with excess of potassic sulphate. The solution, which at first showed the didymium bands, was then found to be free from didymium.

32. The insoluble double sulphates were filtered and washed with a cold saturated solution of potassic sulphate. The precipitate was boiled for some time in ammonia, filtered, dissolved in hydrochloric acid, and precipitated with ammonic oxalate. This precipitate was ignited and tested in the radiant matter tube. It gave scarcely a trace of citron band (23). The earth was further purified by the potash and chlorine method, and was found to consist principally of ceric oxide.

33. The solution filtered from the insoluble potassio-ceric sulphate (31) was boiled with ammonia and ammonic sulphide. A small quantity of a white flocculent earth came down—too small a quantity to weigh. Tested in a radiant matter tube, it gave the citron band better than either of the above precipitates, showing that by this treatment the body had been concentrated (25).

34. It seemed possible that the earth sought for might be present in larger quantity in the thorite, but that it had been gradually carried down mechanically or by mass-action rather than chemically, by the numerous operations it had undergone before getting it to the final stage. Therefore a fresh quantity of thorite was extracted with hydrochloric acid. The solution was precipitated with potassic sulphate, taking the usual precautions to secure complete precipitation. A bulky precipitate ensued, which contained the thorina and cerium earths. These were separated and tested, and found to give only a faint citron band.

35. The solution of earthy sulphates soluble in potassic sulphate was precipitated with ammonic oxalate. The precipitate ignited with sulphuric acid, and tested in a radiant matter tube, gave the citron spectrum with great brilliancy (25, 33).

Chemical facts connected with the citron body.

36. Certain chemical facts concerning the behaviour of the sought-for element which came out during the course of the tentative trials already described had considerably narrowed the list amongst which it might probably be found. All the evidence tended to show that it belongs to the group of earthy metals, consisting of aluminium, beryllium, thorium, zirconium, cerium, lanthanum, didymium, and the yttrium family, together with titanium, tantalum, and niobium. The sought-for earth is insoluble in excess of potash (25); this excludes aluminium and beryllium. It is not precipitated by continued boiling with sodic thiosulphate (17, 27); this excludes aluminium, thorium, and zirconium. Fused with acid potassic sulphate, the resulting compound is readily soluble in cold water; this excludes tantalum and niobium. Evaporating to dryness with hydrochloric acid and heating for some time does not render the mass insoluble in water (27); this excludes titanium and silicium. It is easily soluble in an excess of a saturated solution of potassic sulphate (25, 33, 34); this excludes thorium, the cerium group, some of the numerous members of the

yttrium group, and zirconium. The only remaining elements among which this elusive body would probably be found are those members of the yttrium family which are not precipitated by potassic sulphate.

37. On the other hand, the body giving the citron band spectrum did not behave like one of the known earths. A rich residue was fused with sodic carbonate, and the mass extracted with water. The insoluble residue, on testing in the usual way, was rich in citron band, but subsequent treatment of the aqueous solution gave me an earth which also gave the citron band strongly.

An acid solution of the citron body was precipitated by ammonia and ammonic chloride. The earth was not completely precipitated, but after a long boiling some remained in solution. I have since ascertained that the detection of the citron-band body in solution under these circumstances is only owing to the marvellous delicacy of the test, which carries our powers of recognition far beyond the resources of ordinary chemistry.

38. Besides obtaining indirect evidence that the citron band was not due to certain elements, I tried special experiments with each substance, brought to the highest possible state of purity. In many cases I detected more or less traces of citron band; but I had come to the conclusion, abundantly warranted by facts, that this citron band was an extraordinarily sensitive test of the presence of the element causing it; and the minute chemistry of many of these earthy metals being insufficiently known, it was not surprising that traces of one of them should adhere to another in spite of repeated attempts to purify it out. With each successive fractional precipitation the citron band became fainter, showing that with perseverance the last trace would probably disappear. The time this process would have occupied, in my opinion, seemed not worth the little additional evidence it would have afforded.

39. Taking into consideration the extremely small quantity of phosphorescent material which had so far been obtained, all these experiments justified me in assuming that the body sought for not only belonged to the group of earths, but also most probably to the sub-group not precipitated by potassic sulphate to which yttria belongs. As, however, the number of these metals has increased so much within the last few years, and as the quantity of material which I had up to the present at my disposal was too small to admit of a satisfactory chemical examination being made of it, search was commenced among other sources known to be rich in these metals. Besides, not only did the majority of the substances I had up till now obtained in anything like quantity indicate the citron band earth to belong to the yttria group (33, 34, 36), but also that either the earth itself showed an absorption band in the spectroscope, or was invariably accompanied by one which did. On the other hand, I had a certain amount of evidence that the earth sought for did not show a band in the spectroscope (24); but remembering the extremely small quantity of very impure substance experimented with, the evidence on this point was not at all conclusive.

The sought-for body one of the yttrium family.

40. The yttria earths form a somewhat numerous family. Fortunately for chemists, a mineral rich in yttria earths—samarskite—has been found in large quantity in Mitchell County, North Carolina, and to this mineral I accordingly now directed my attention.

The following list of elements of the yttrium and its allied families, said to occur in samarskite and similar minerals, may be considered complete to the present time.

Name.	Absorption Spectrum.	Hydrogen equivalent of Metal.(1) (Type of Oxide M_2O.)
Cerium	No	47·1(2)
Columbium(3)	Yes	—
Decipium	Yes	57·0(4)
Didymium	Yes	48·5(5)
Didymium β	Yes	47·0(6)
Erbium	Yes	55·3(7)
Holmium(8)	Yes	54·0(9)
Lanthanum	No	46·0(10)

(1) As it is at present doubtful whether the oxides of several of the metals in this table belong to the type M_2O, M_2O_3, or MO, I have, for the sake of uniformity and simplicity, in calculating the values from the composition of their salts, by which these metals are chiefly discriminated, taken the type of oxide to be M_2O.

(2) Bunsen, 'J. Pr. Chem.,' ser. 2, vol. xii., p. 209.

(3) Dr. J. Lawrence Smith in a paper read before the United States National Academy of Sciences in 1879, announced the discovery in Samarskite of two new elements, which he named Columbium and Rogerium ('Nature,' vol. xxi., p. 146). I have failed to find any further notice of these elements. This Columbium must not be confounded with the well-known Columbium, sometimes called Tantalum.

(4) Delafontaine, 'Comptes Rendus,' vol. lxxxvii., p. 632, vol. xciii., p. 63; 'Chemical News,' vol. xxxviii., p. 223, vol. xliv, p. 67.

(5) Clève, 'Bull. Soc. Chim.,' ser. 2, vol. xxi., p. 246; Brauner, 'Comptes Rendus,' vol. xciv., p. 1718; 'Chemical News,' vol. xlvii., p. 175.

(6) Clève, 'Comptes Rendus,' vol. xciv., p. 1528; 'Chemical News,' vol. xlv., p. 273. Brauner, 'Comptes Rendus,' vol. xciv., p. 1718; 'Chemical News,' vol. xlvi., p. 16.

(7) Clève, 'Comptes Rendus,' vol. xci., p. 381; 'Chemical News,' vol. xlii., p. 199. Lecoq de Boisbaudran, 'Comptes Rendus,' vol. lxxxix., p. 516; 'Chemical News,' vol. xl., p. 147.

(8) Called by Soret, the first discoverer, "X." Subsequently Clève discovered the same metal and called it holmium. Soret has now adopted Clève's name. 'Comptes Rendus,' vol. lxxxix., p. 708, and vol. xci., p. 378; 'Chemical News,' vol. xl., p. 224, and vol. xlii., p. 199. Lecoq de Boisbaudran, 'Comptes Rendus,' vol. lxxxix., p. 516; 'Chemical News,' vol. xl., p. 147.

(9) Clève, 'Comptes Rendus,' vol. lxxxix., p. 478; 'Chemical News,' vol. xl., p. 125.

(10) Brauner, 'Comptes Rendus,' vol. xciv., p. 1718; 'Chemical News,' vol. xlvi., p. 16.

Name.	Absorption Spectrum.	Hydrogen equivalent of Metal. (Type of Oxide M_2O).
Mosandrum	No	51·2[11]
Philippium [12]	No	—
Rogerium[13]	Yes	—
Samarium	Yes	50·0[14]
Scandium	No	14·7[15]
Terbium	No	49·5[16]
Thorium	No	58·4
Thulium	Yes	56·5[17]
Ytterbium	No	57·9[18]
Yttrium	No	29·7[19]
Yttrium α	No	52·2[20]
Yttrium β	Yes	49·7[21]
Zirconium	No	22·5

(11) Lawrence Smith, 'Comptes Rendus,' vol. lxxxvii., pp. 145, 146, 148. Marignac, *ibid.*, vol. lxxxvii., p. 281. Delafontaine, in October, 1878 (*ibid.*, vol. lxxxvii., p. 600), considers mosandrum a mixture of terbium, yttrium, erbium, didymium, and philippium. Subsequently, however, Lawrence Smith, in November, 1878 (*ibid.*, vol. lxxxvii., p. 831), adduces chemical and other reasons to show that his mosandrum is not a mixture, but a true element. A year later, September 1, 1879 (*ibid.*, vol. lxxxix., p. 480), Lawrence Smith repeats the claim for mosandrum to be classed with the elements.

(12) Delafontaine, 'Comptes Rendus,' vol. 87, p. 559; 'Chemical News,' vol. 38, p. 202; 'Jour. Chem. Soc.,' vol. 36, p. 116.

(13) *See* Note (3) to Columbium, *ante*.

(14) Lecoq de Boisbaudran, 'Comptes Rendus,' vol. lxxxviii., p. 322, and vol. lxxxix., p. 212; 'Chemical News,' vol. xxxix., p. 115, and vol. xl., p. 99. Brauner, 'Chemical News,' vol. xlvii., p. 175; Clève, 'Comptes Rendus,' vol. xcvii., p. 94; 'Chemical News,' vol. xlviii, p. 39.

(15) Nilson, 'Comptes Rendus,' vol. xci., p. 118; 'Chemical News,' vol. xlii., p. 83. Clève, 'Comptes Rendus,' vol. lxxxix., p. 419; 'Chemical News,' vol. xl., p. 159.

(16) Marignac, 'Ann. Chim. et Phys.,' ser. 5, vol. xiv., p. 247; 'Journ. Chem. Soc.,' vol. xxxvi., p. 113. Delafontaine, 'Ann. Chim. et Phys.,' ser. 5, vol. xiv., p. 238; 'Journ. Chem. Soc.,' vol. xxxvi., p. 114.

(17) Clève, 'Comptes Rendus,' vol. lxxxix., p. 478, and vol. xci., p. 328; 'Chemical News,' vol. xl., p. 125, and vol. xlii., p. 182. Thalén, 'Comptes Rendus,' vol. xci., p. 376; 'Chemical News,' vol. xlii., p. 197.

(18) Marignac, 'Comptes Rendus,' vol. lxxvii., p. 578; 'Chemical News,' vol. xxxviii., p. 213. Nilson, 'Comptes Rendus,' vol. lxxviii., p. 642, vol. xci., p. 56; 'Chemical News,' vol. xlii., p. 61.

(19) Clève, 'Comptes Rendus,' vol. xcv., p. 1225; 'Chemical News,' vol. xlvii., p. 4. 'Bull. Soc. Chim.,' vol. xxxix., p. 120; 'Chemical News,' vol. xlvii., p. 143.

(20) Marignac, 'Comptes Rendus,' vol. xc., p. 899; 'Chemical News,' vol. xli., p. 250.

(21) This is almost certainly identical with Lecoq de Boisbaudran's samarium. See Marignac, 'Comptes Rendus,' vol. xc., p. 899; 'Chemical News,' vol. xli., p. 250. Soret, 'Comptes Rendus,' vol. xci., p. 378; 'Chemical News,' vol. xlii., p. 199.

41. Some of these claimants will certainly not stand the test of further scrutiny. Thus samarium and yttrium β are in all probability identical; and I should scarcely have included philippium, as Roscoe* has conclusively proved that this is a mixture of terbium and yttrium, and my own results (61) confirm those of Roscoe. Moreover, others of these so-called elements will probably turn out to be mixtures of known elements. But in the confessedly very imperfect state of our knowledge of the chemistry of these metals it is not safe for me in this research to assume that any one of them will surely not survive. The complete list as it stands will therefore be taken to contain all hitherto claimed as new, although it is almost certain to include too many.

The sought-for body has no absorption spectrum.

42. In the second column "Yes" or "No" indicates whether the solutions give an absorption spectrum when examined by transmitted light. Now could I definitely settle whether solutions of the citron-band body gave an absorption spectrum or not, I could at once eliminate a whole class of elements.

This was not difficult to determine. I have already said (22, 24) that spectroscopic examination entirely failed to detect didymium in many solutions of the earth which gave the citron band strongly. This was not always the case. In early days of this research I frequently obtained absorption bands innumerable when the citron-band body was known to be present; but as I became better acquainted with the chemical reactions of the new earth I gradually succeeded in eliminating one after the other those metals yielding absorption spectra. The earth from zircons (18, 21) gave the most satisfactory results in this respect. This, after removing the little didymium present, gave but a trace of an absorption spectrum, which from its general appearance was probably due to erbia. The earth obtained from cerite (25), which gave the citron spectrum with great brilliancy, on the other hand yielded no absorption spectrum; and generally I may say that, whenever I started with a sufficient quantity of an earth giving both citron-band spectrum and absorption spectrum, I could, by appropriate chemical means, always separate it into three portions,—one which gave the citron-band spectrum with great brilliancy, and showed in concentrated solution a very faint absorption spectrum, and frequently none at all; another which gave very little citron-band spectrum, but a good absorption spectrum; and a third intermediate portion—about four-fifths of the whole—which gave both citron band and absorption spectrum. This portion, by repetition of the treatment, could again be split up in the same way, and the operation repeated as often as the stock of material held out.

43. Having definitely settled the question that the metal giving the citron-band spectrum was not one of those giving an absorption spectrum, the possible elements become materially narrowed to the following list:—Cerium, lanthanum, mosandrum, scandium, terbium, thorium, ytterbium, yttrium, yttrium α, and zirconium.

* 'Jour. Chem. Soc.,' vol. 41, p. 277.

Of these the potassic sulphate reaction (36) excludes cerium, lanthanum, scandium, thorium, yttrium α, and zirconium, so there are left only the following :—

Mosandrum,
Terbium,
Ytterbium,
Yttrium.

44. Certain chemical reactions for a long time made me dismiss yttrium from the list of likely bodies. In my analysis of zircons (18), towards the latter part of the process, I used the following process to separate the iron :—The solution, mixed with tartaric acid and excess of ammonia, was allowed to stand for some time. A small quantity of a precipitate gradually formed, which was filtered off, and it was this filtrate, after separating the iron with ammonic sulphide, that yielded the greatest quantity of substance giving the citron band. Now one of the methods of separating yttria from alumina, berylla, thoria, and zirconia is to precipitate it as tartrate in the presence of excess of ammonia, the other earths remaining in solution. FRESENIUS says :—"The precipitation ensues only after some time, but it is complete."

The precipitate thus obtained with tartaric acid and ammonia should therefore contain all the yttria: *it gave no citron band whatever in the radiant matter tube;* whilst the residue, which should be free from yttria (18), proved for a long time the only source of material wherewith to investigate the chemical properties of the body giving the citron spectrum.

45. Another reason which made me, at this stage of the research, pass over yttria, was that I had already tested this earth in the radiant matter tube. In a paper on "Discontinuous Phosphorescent Spectra in High Vacua," read before the Royal Society, May 19th, 1881,* I said—"Yttria shows a dull greenish light giving a continuous spectrum" (75).

For these reasons I for a long time omitted yttria from my list of possible bodies, and considered that the earth, if not a new one, might turn out to be either mosandra, terbia, or ytterbia.

Analysis of samarskite.

46. A very large quantity (about 15lbs. weight altogether) of samarskite was worked up, partly by the hydrofluoric acid method of LAWRENCE SMITH,† and partly by fusion with potassic bisulphate. The niobic and tantalic acids after purification were found to give no citron band spectrum.

These methods both gave as a result a large quantity of mixed earths containing most, if not all, of the bodies enumerated in par. 40. Tested in the radiant matter tube, this material gave the citron spectrum very brilliantly. It was dissolved in hydrochloric acid, neutralised as nearly as possible with ammonia, and boiled with

* Proc. Roy. Soc., No. 213, 1881.

† 'Comptes Rendus,' vol. 87, p. 146.

sodic thiosulphate. This precipitated the thoria, zirconia, and alumina. In this precipitate some of the scandia might also be found, if present in quantity, but as scandic thiosulphate is not completely precipitated, and the earth is present only in minute traces, not much scandia, it is probable, was thus carried down.

This thiosulphate precipitate, treated in the usual way with sulphuric acid, gave no citron band in the radiant matter tube.

47. The filtrate from the thiosulphate was precipitated hot with excess of ammonia, and the precipitate after washing treated with sulphuric acid, dried, and heated till fumes of sulphuric acid disappeared. The sulphate, whitish with a very pale rose tint, was finely ground, and dissolved with frequent agitation in the smallest possible quantity of cold water—an operation which required much time. The solution was then precipitated with potassic sulphate, taking all necessary precautions to keep the liquid well saturated with potassic sulphate. This operation was allowed to go on for about ten days, when the precipitated double sulphates were filtered off and slightly washed with a saturated solution of potassic sulphate. The precipitate contained cerium, lanthanum, didymium, didymium β, decipium, samarium, scandium, yttrium α, yttrium β, together with any thorium and zirconium which might have escaped the thiosulphate treatment.

48. The filtrate from the double sulphates was precipitated hot with ammonia, which brought down the erbia, holmia, mosandra, terbia, thulia, ytterbia, and yttria. The small quantity of manganese in solution was in this operation completely thrown out.

49. The insoluble double sulphates (45) were dissolved in hydrochloric acid, precipitated hot with ammonia, washed till free from potassium salts, re-dissolved, precipitated as oxalates, ignited, and set aside for further examination. On testing in the radiant matter tube this mixture of oxides was found to be practically free from citron band.

50. The ammonia precipitate from the sulphates soluble in potassic sulphate (46) was well washed till free from potassium salts, and dissolved in excess of nitric acid. The concentrated solution gave an absorption spectrum showing lines belonging to erbium and allied metals. Having already proved that the body I was seeking was not one of those metals which gave an absorption spectrum (42, 43), my first object was to find some method by which I could roughly separate this mixture of earths into two portions, one giving absorption bands, and the other having no action on the transmitted spectrum. I found this was possible by taking advantage of the different solubility of the oxalates in nitric acid.

51. The highly acid solution of the nitrates was fractionally precipitated in the following manner:—

To the boiling liquid a solution of ammonic oxalate was added drop by drop. The precipitate at first formed re-dissolved on stirring. The cautious addition of ammonic oxalate was repeated until the precipitate refused to dissolve entirely, but left the hot liquid somewhat milky. It was then rapidly cooled with constant stirring, which

brought down a heavy crystalline oxalate. This was filtered off, and called oxalate A. The filtrate, again heated to boiling, was precipitated in exactly the same way with a further quantity of ammonic oxalate till the hot liquid became opalescent. On cooling and stirring, a farther quantity of oxalate came down. The filtrations and precipitations were repeated until no more precipitate could be obtained. Usually I could get twelve or thirteen fractionations in this manner; towards the end the solution did not get milky, and it had to stand sometimes twenty-four hours before much oxalate came down.

52. The fractions first precipitated by oxalic acid gave very strong absorption bands when the concentrated solutions of the oxides were examined by transmitted light. The fractions last precipitated showed the absorption bands only faintly.

53. These operations gave me oxalates from A to L. These, ignited, with free access of air, were then each dissolved in nitric acid, and again separately fractionated as oxalates. The result was about 150 precipitates, ranging from A_1 A_2 . . . A_{12}, B_1 B_2 . . . B_{12}, to L_1 L_2 . . . L_{12}.

These, after ignition, were separated into five lots according to order of colour, and the fractionation of each of the five lots repeated as already described; the series of operations now closely resembling those of PATTINSON'S process for desilvering lead. This gave me about sixty lots. This time the hydrogen equivalent of the metal of each lot was taken by converting the oxalate into sulphate and estimating the sulphuric acid, assuming M_2O to be the type of oxide (40, note 1). The result was a series of earths having hydrogen equivalents (M) ranging from about 48 to 33. The earths were now sorted into high, low, and intermediate, those giving intermediate H equivalents being re-fractionated with repeated H equivalent estimation, the highest and lowest being each time separated and added to the former high and low lots.

54. The ultimate result of about five hundred fractional precipitations gave me a mixture of earths having an H equivalent M=48, and showing a strong absorption spectrum (56); a mixture having an H equivalent M=33, having no absorption spectrum (65); and intermediate earths.

In the radiant matter tube all these fractions gave the citron-band spectrum well, but that of the earth of lowest equivalent was much the brightest, and that of the highest equivalent the least intense.

55. Three methods are available for the partial separation of these earths and for the complete purification of any one of them. The formic acid process (56, 57) is best for separating terbia, as terbic formate is difficultly soluble in water, the other formates being easily soluble.

Fractional precipitation with oxalic acid (63, 64, 65) separates first erbia, holmia, and thulia, then terbia, and lastly yttria. This is the only method which is applicable for the separation of small quantities of terbia from yttria.

Fusing the nitrates (60, 68, 69) separates ytterbia, erbia, holmia, and thulia from yttria. It is not so applicable when terbia is present, and is most useful in purifying

the gadolinite earths. This process is the only one known for separating ytterbia from yttria.

Selection must be made of these methods according to the mixture of earths under treatment, changing the method as one earth or the other becomes concentrated on one side or thrown out on the other. Each operation must be repeated many times before even approximate purity is attained. The operations are more analogous to the separation of members of homologous series of hydrocarbons by fractional distillation than to the separations in mineral chemistry as ordinarily adopted in the laboratory.

Preparations of pure terbia.

56. The mixture of high equivalent earths (54) richest in terbia, erbia, holmia, and thulia was treated as follows:—

The earths were dissolved in dilute formic acid, and the solution heated for some time. A white powder of terbic formate separated. This was filtered off, the solution containing the more easily soluble formates evaporated to dryness, and ignited. In this way the M=48 earths were separated into two lots, one rich in terbia and the other rich in erbia, &c. The treatment with formic acid was again repeated on both lots, and the crude terbia finally purified as follows:—

57. The crude terbia from all the operations was systematically treated by the formic acid process, keeping the liquid so dilute that only a portion of the terbic formate separated out each time. The syrupy solution of formates was treated as described further on (60). The hydrogen equivalent of the terbium was taken each time; latterly it kept pretty constant at 49·5. The terbia was also tested in the radiant matter tube. At first the citron spectrum was very strong; gradually, however, it got fainter and fainter under the repeated formic treatment, until finally the spectrum became so weak as to satisfy me that it was due only to impurity in the terbia, and that, had the material been sufficient to stand against the extravagant process of purification adopted, I should finally have got a terbia giving no citron-band spectrum. (Subsequent examination (87) showed me that this terbia did not contain more than 1-5000th part of yttria.)

58. A concentrated solution of the purest terbia obtained in this way, when examined by the spectroscope, showed no absorption lines whatever: proving the absence of erbium, holmium, and thulium.

59. The hydrogen equivalent (49·5) would not definitely show the absence of ytterbium (57·9) and yttrium (29·7); but these would have been separated by the formic acid treatment, terbic formate requiring 30 parts of water for its solution, whilst yttric and ytterbic formates dissolve in less than their own weight of water. Moreover, it was not probable that the terbia contained an appreciable quantity of any of these earths as an impurity, for neither the oxalic acid, the fusing nitrate, nor the formic acid process of fractionation produced any change in the atomic weight, 49·5.

Preparation of mixed erbia, holmia, and thulia free from other earths.

60. The filtrate from the terbic formate (57), rich in erbia, and containing besides terbia, holmia, thulia, and yttria, was now treated by converting it into nitrates, evaporating to dryness, and submittting the mass to careful fusion, stopping the operation when the liquid mass began to evolve nitrous fumes. The erbic, holmic, and thulic nitrates decomposing before the yttric nitrate, extraction with water gave an insoluble residue rich in erbia, holmia, and thulia, and a filtrate rich in yttria. The insoluble residue was dissolved in nitric acid, again evaporated to dryness, and fused. These operations were repeated eight or ten times, with the result of raising the H equivalent of the erbium metals to about 56·8, but the citron-band spectrum remained strong for some time after. It, however, ultimately disappeared. A concentrated solution of this erbic, &c., nitrate showed a beautiful and intense absorption spectrum. I did not attempt any separation of erbium, holmium, and thulium from each other, as the evidence here obtained is sufficient to show that the element giving the citron-band spectrum is not one of these three metals. Likewise I had far too little material to enable me to enter on a work of such difficulty with any prospect of success.

Philippia.

61. The so-called philippia was sought for in the portion of earths intermediate between the terbia and yttria (54). These were dissolved in dilute formic acid, and the solution, filtered from some terbic formate which would not dissolve, was carefully evaporated down to a small bulk, filtering off the terbic or other difficultly soluble formates as they deposited. The clear concentrated solution was then set aside over sulphuric acid to crystallise. In the course of a few days brilliant rhombic prisms crystallised out, having exactly the appearance described by DELAFONTAINE.* The finest of these crystals were picked out, dried on blotting-paper, and analysed. The hydrogen equivalent was found to be M=38·2. The citron-band spectrum in the radiant matter tube was very brilliant. The solution decanted from these crystals was evaporated to a syrupy consistency, filtered from insoluble terbic formate which deposited, and treated for yttria (65).

Some of the best rhombic crystals were added to cold water acidulated with formic acid, and gently heated, but all attempts to dissolve and re-crystallise them failed. A large quantity of an insoluble formate separated, and the mother-liquor on concentration again deposited shining rhomboidal crystals. On attempting to re-crystallise these, they again deposited an insoluble white powder. The mother-liquor was found to contain a large quantity of yttria, and the white insoluble formate on ignition gave an earth having the atomic weight and chemical behaviour of terbia. This entirely

* 'Comptes Rendus,' vol. 87, p. 559; 'Chemical News,' vol. 38, p. 202; 'Journ. Chem. Soc.,' vol. 36, p. 116.

corroborates Professor Roscoe's conclusions,* that Delafontaine's philippia is nothing but a mixture of yttria and terbia.

Mosandra.

62. The chemical characters of this earth are so little known that I could not attempt to search for it. But as the citron band-forming earth always appeared concentrated amongst those whose double sulphates were most soluble in potassic sulphate,—and, of these, amongst those having the palest colour and lowest atomic weight,—it was scarcely conceivable that the earth I was in search of should ultimately prove to be one whose properties did not in any case correspond to these,—of a dark orange yellow colour, forming a difficultly soluble double potassic sulphate, and having the very high equivalent of M=51·2; these being the properties ascribed to mosandra by the discoverer, Professor Lawrence Smith.

Separation of terbia and yttria from erbia, holmia, and thulia.

63. The mother-liquors, from which as much terbic formate as possible had been separated by the process above described (56, 57), were now evaporated down with nitric acid till all the formates were decomposed, and the highly acid solutions of nitrates were fractionally precipitated with oxalic acid (51, 52, 53).

64. The erbic, holmic, and thulic oxalates come down first; then the terbic oxalate; lastly the yttric oxalate (53). After repeated fractional precipitations I at last succeeded in obtaining a mixture of yttria and terbia of a golden colour, which gave a very brilliant phosphorescent spectrum in the radiant matter tube, but showed no trace of absorption band when the concentrated solution of the nitrates was examined in the spectroscope.

Separation of terbia and yttria.

65. The crude yttria was now added to the mixture of earths (54) having a hydrogen equivalent M= 33, and the whole submitted again to fractionation with oxalic acid, in a somewhat modified manner.

An excess of strong nitric acid was added to the solution of mixed terbic and yttric nitrates, and the solution was heated to the boiling point. Strong oxalic acid solution was added drop by drop till a faint permanent precipitate was produced. Strong nitric acid was now added, a drop at a time, till the solution again became clear, and the whole was allowed to cool very slowly without agitation. On cooling, an oxalate crystallised out in brilliant prisms. These contained nearly all the terbia with some of the yttria, whilst the mother-liquor contained most of the yttria with a little terbia. The filtrate was treated with more oxalic acid, a fresh crop of crystals being produced,

* 'Jour. Chem. Soc.,' vol. 41, p. 277.

when the crystals were ignited, and the resulting earths re-treated with nitric acid and oxalic acid. After repeated fractionations I finally obtained in this manner a perfectly white yttria and a terbia containing a small quantity of yttria. This terbia was added to the crude terbia from previous operations, and purified as already described (57).

These operations gave me two earths,—yttria and terbia,—which, from the constancy of their H equivalents, were taken to be pure. The earths giving absorption spectra and having H equivalents other than 29·7 and 49·5, include erbia, holmia, and thulia. This portion was not further examined for the purposes of this investigation.

Ytterbia.

66. Before considering it finally proved that the substance forming the citron-band spectrum was yttria, it was necessary to prepare ytterbia and ascertain its behaviour in the radiant matter tube, this earth and yttria being the only remaining earths to which the citron spectrum could possibly belong.

The two metals have hydrogen equivalents—ytterbium 57·9 and yttrium 29·7. The chemical reactions are also sufficiently different to render their separation a matter of no very great difficulty.

67. Gadolinite is said by NILSON to contain most ytterbia, so this mineral was chosen in preference to samarskite. The crude earths were first purified from all the earths whose sulphates are difficultly soluble in potassic sulphate (22, 25, 31 to 36), then by the formic acid process from terbia (56, 57), and lastly by fractional precipitation with oxalic acid from the erbia earths (65). There remained an almost white yttria, which gave the citron-band spectrum very brilliantly. Now, gadolinite contains only about 0·1 per cent. of ytterbia, and about 35 per cent. of yttria; therefore the ytterbia to yttria in this mixture was somewhat in the proportion of 1 to 300, and it gave the citron-band spectrum as brillantly as I had ever seen it. The probability was that the earth forming nearly the whole was the one giving the spectrum.

68. Ytterbic nitrate decomposes on fusion almost as easily as erbic nitrate (60), whilst yttric nitrate resists decomposition much more energetically.* Fusion of the nitrates is also the best process for throwing out the erbia, holmia, and thulia, and is therefore the best for purifying gadolinite yttria, as this mineral is rich in the erbia earths and contains little terbia.

The gadolinite yttria was converted into nitrate, fused for a short time, and extracted with water. The portions soluble and insoluble in water were again separately submitted to this treatment, until at last a colourless earth was obtained, the nitrate of which decomposed easily on fusion, and another whose nitrate resisted decomposition when exposed for a long time to nearly a red heat (70).

The earth from the easily decomposed nitrate gave at first a faint citron-band

* MARIGNAC, 'Comptes Rendus,' vol. 90, p. 902.

spectrum, evidently due to impurity. On repeating the operation several times I at last succeeded in obtaining a white earth which gave only the merest trace of citron-band spectrum. Its hydrogen equivalent, 58·0, and its chemical properties showed that it was probably MARIGNAC's ytterbia. Subsequent experiments satisfied me that this earth did not contain more than 1-10,000th part of yttria (84, 87). The extreme tediousness of the chemical operations necessary to obtain this high degree of purity, and the long time they require, prevented me from pushing these results beyond what was necessary to prove the special point at issue.

Purification of yttria.

69. The white earth obtained in the operation described at par. 65 might still contain traces of terbia, together with erbia, holmia, and thulia. I had relied on the absence of absorption spectrum as proving the absence of erbia, holmia, and thulia, but this test is not a very delicate one, and a final purification was therefore attempted. The decomposition of the fused nitrates was now the process relied on for this final purification, the yttric nitrate resisting nearly a red heat without decomposition, whilst the erbic, holmic, and thulic nitrates are decomposed at a much lower temperature. The operation was carried on as described at par 60.

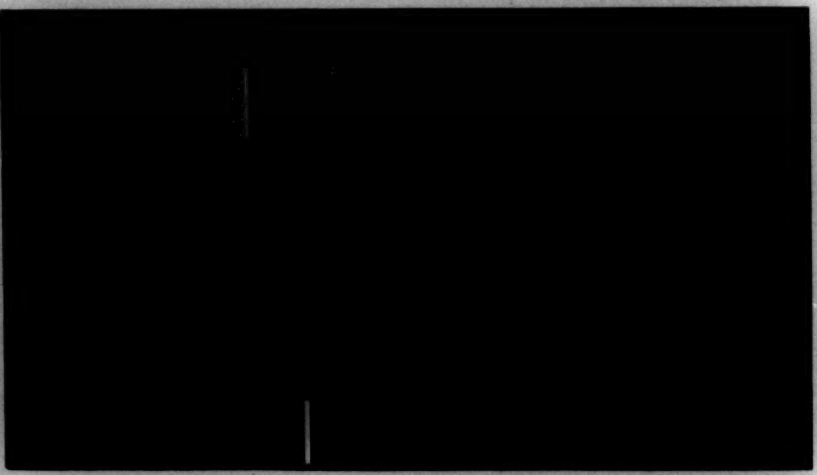
The yttric nitrate left undecomposed, after repeated fusions, was now fused at a higher temperature, extracted with water, filtered from insoluble residue, and the operation repeated on the filtrate. After several such operations the H equivalent of the yttria was taken at every succeeding operation, and the spectral appearance in the radiant matter tube was also examined. The equivalent gradually got down to 31·0, but the spectra did not vary very much; that from the earth of lowest equivalent being, however, the most brilliant.

70. The yttric nitrate, prepared from gadolinite and freed from ytterbia by the fusion of the nitrates (68), was converted into oxalate and ignited. The resulting yttria was quite white, and on testing in the radiant matter tube gave a spectrum absolutely identical with that given by the zircon (18), cerite (25), thorite and orangite (33, 34), and samarskite (64, 69), yttrias. Pure yttria was also prepared from yttro-tantalite, euxenite, allanite, tyrite, and also from plaster of Paris (15) and common limestone. In no case could I detect any difference in the position or intensity of the lines shown by their phosphorescent spectra.

The phosphorescent spectrum of yttria.

71. The spectrum shown by pure ignited yttric sulphate in a radiant matter tube is one of the most beautiful objects in the whole range of spectroscopy. The lines are not so sharp as those given by spark spectra, but are more like the flame spectra

of the alkaline earths. The spectrum is best seen under low dispersion and not too narrow a slit. The accompanying cut gives an accurate map of the spectrum. I have given in line No. 1 the position of the principal FRAUNHOFER lines for comparison of position. Line No. 2 gives the position of the bands, and No. 3 the relative intensities represented by the heights of the ordinates. The numbers along the top refer to a scale of squared oscillation frequencies, or of the squared reciprocals of wave lengths.



72. Commencing at the red end, two narrow faint bands are seen at 2245 and 2275, followed by a stronger and broader red band extending between 2355 and 2415. Another faint band occurs between 2577 and 2610, followed after a very narrow black interval by a stronger reddish-orange band extending to 2627. Another faint orange band occurs at about 2800, with edges too indistinct for measurement. At about 2940 a faint yellow band appears, extending to about 3025. The strong citron-coloured band follows closely from 3028 to 3049; and a little further on, between 3100 and 3120, a much fainter citron band is seen. Two characteristic green bands follow after a dark interval; the first, very bright, extending between 3312 and 3320, but shading off on each side; the second somewhat fainter, but more sharply defined than the first, extending from 3420 to 3440; there is also a third faint green band, between 3460 and 3467. At 3730 is the centre of a narrow and faint

bluish-green band; at 4110 to 4125 in a blue band; and at 4296 another blue band commences, and, extending a short distance, fades away so gradually as to render measurement of the further side impossible. At 5052 and 5351 are two violet lines, but they are not sufficiently sharp to enable accurate measurements to be taken.

I have carefully compared the spark spectrum given by yttric chloride with the phosphorescent spectrum, and have not found any similarity between them, neither have I detected any discontinuity of spectrum on examining the faint light shown by yttrium compounds in BECQUEREL'S phosphorescope.

73. The above description applies to the spectrum shown either by pure yttria or by an earth tolerably rich in yttria. When traces are present the citron band only is seen. A little more yttria brings out the first and then the second green band, and finally, as the proportion of yttria increases, the red and blue bands appear (80 to 86).

Circumstances modifying the yttria spectrum.

74. In the early days of this investigation I frequently found that an earthy mixture which by one mode of treatment gave no spectrum, would give a good citron band by a modification of the treatment, and I gradually found that I was most likely to get the spectrum when the body had been treated with sulphuric acid and then ignited to dull redness (4). Not knowing the circumstances governing the appearance of the citron band, it would not then have been safe to have altered this mode of treatment. Now, however, having ascertained the earth to which the spectrum was due, and having a considerable quantity at my disposal, experiments were tried on other methods of treating yttria before exposing it in the radiant matter tube.

75. Pure yttria precipitated by ammonia from the sulphate was dried at a temperature below redness and tested. It did not phosphoresce in the slightest degree, and, necessarily, no citron-band spectrum was to be seen. The yttria was removed from the tube, converted into sulphate, heated to redness, and again tested. It now gave the citron band magnificently. This shows what apparently trivial circumstances will alter the whole course of an investigation. In 1881, when searching for discontinuous phosphorescent spectra, I tried a similar experiment with pure precipitated yttria (45), and entirely missed its citron-band spectrum. Had I first treated the yttria with sulphuric acid, instead of testing the earth itself in the radiant matter tube, the results would have been very different, and this research would probably have never been undertaken.

76. Yttria was now prepared by igniting the precipitated oxalate at a red heat. On testing in the radiant matter tube it phosphoresced with feeble intensity, the light being about one-twentieth of that given by the ignited sulphate under similar conditions. The citron band was almost as sharp as the sodium line, and was shifted one division towards the blue end, now occupying the position 3050 to 3060, its

former place 3028 to 3049 being quite dark. The appearance is shown in line No. 4. On superposing this spectrum and that from the ignited sulphate the displacement of the citron bands was clearly observed; with a very narrow slit the two bands were seen not to touch. The two green bands were visible, but very hazy and indistinct, and only to be resolved into bands with difficulty. The yttria was now removed from the tube, ignited to a bright red heat, and re-tested. The spectrum was a little stronger than that given by the yttria ignited at a lower temperature, but in other respects the general appearance and measurements were unchanged. No alteration was caused by subsequent ignition to a white heat.

77. Pure yttric sulphate ignited to a bright white heat gave a spectrum corresponding to the oxide (76); the sulphate having been decomposed by the high temperature.

78. Yttric phosphate was precipitated, washed, and dried at a heat below redness, and introduced into the radiant matter tube. It phosphoresced faintly, giving the citron band hazy and faint, extending from about 3010 to 3060. The red bands were faint, and the green bands, especially the first one, were stronger than usual. The salt was now removed from the tube, and heated to redness. It became of a grey colour, and now phosphoresced with a beautiful green light. The citron band was still broad and faint, but the green bands were very bright and distinct, and the red band between 2610 and 2627 was also stronger. The spectrum No. 5 shows the appearance.

Heating the phosphate before the blowpipe made little change in the character of the phosphorescence. It was moistened with sulphuric acid, heated to a dull redness, and then tested, but no further change was produced in the spectrum. This experiment shows that the citron-band test for yttrium is far less delicate in the presence of phosphoric acid than in its absence.

Occurrence of yttria in Nature.

79. It is an old and probably a true saying that every element could be detected everywhere had we sufficiently delicate tests for it. Early observations (10, 16) had prepared me for the wide distribution of the element giving the citron band, and no sooner had the exquisite sensitiveness of this spectrum test forced itself on my notice than I sought for yttrium in other minerals. Facts which I had noticed in connexion with the variation of the appearance of the citron spectrum, according to the quantity of yttrium present, showed that it might be possible to devise a process for the rough quantitative estimation of yttrium, and after several experiments this was ultimately carried out in the following manner:—

The calcic carbonate which was found to give no citron band (12) was boiled in a quantity of nitric acid insufficient to dissolve it. The solution was filtered from the insoluble residue, diluted to a convenient bulk, and standardised: 14·91 grains of

solution contained 1 grain of calcium. This operation was performed in a room in which had been no yttria compound, and the chemicals and apparatus were new, and had not been taken into the general laboratory. A portion of the standard solution was precipitated with ammonic oxalate, and the calcic oxalate ignited and treated with sulphuric acid. Tested in the radiant matter tube it gave no citron band.

Pure yttric sulphate was dissolved in water to such a strength that 3,000 grains of solution contained 1 grain of yttrium.

80. The solutions were mixed together in the proportion of 1 of yttrium to 100 of calcium, evaporated to dryness, and ignited with sulphuric acid, and the residue tested in a radiant matter tube. The spectrum was bright, the citron band, the two green bands, the blue, and the red bands showed distinctly.

81. A mixture was now prepared in the proportion of 1 of yttrium to 500 of calcium, and tested as above. The citron band was strong, but the green bands were fainter; the blue bands were still visible.

82. A mixture containing 1 of yttrium to 1000 of calcium was next prepared. In the radiant matter tube the citron band was almost as strong as in the last experiment, but the edges were not so sharp, the blue bands were faint, and the green bands had disappeared.

83. A mixture containing 1 of yttrium to 5000 of calcium tested in the radiant matter tube showed the citron band still very bright, but hazy about the edges. No other bands were seen.

84. A mixture of 1 yttrium and 10,000 of calcium was now tried. The citron band was still decided, but not at all sharp.

85. One of yttrium to 100,000 of calcium was next prepared and tested. The citron band was faint, but easily seen. It could not, however, be obtained at all sharp, and appeared broader than usual.

86. A mixture of 1 of yttrium and 1,000,000 of calcium was lastly prepared, and tested in the radiant matter tube. The citron band was very faint, but there was no mistaking its presence, and with care I have no doubt a smaller quantity than 1 in 1,000,000 could be detected. This, however, appears to be near the limit of the test.

87. These seven tubes were mounted on a board, so that connexion with the induction coil could rapidly be made to either of them; and various minerals, &c., were prepared and tested in radiant matter tubes (10). By comparing their spectra with those of the standard tubes I could, after a little practice, determine roughly the proportion of yttrium present, supposing the test not to be interfered with by the presence of phosphoric acid (78).

88. The following are some of the most interesting results obtained in this way:—

		Parts.
Pink coral (one particular specimen)	One part of yttrium in	200
Strontianite	One " "	500
Stilbite	One " "	500
Hydrodolomite, from Vesuvius	One " "	500
Witherite	One " "	1000
Arragonite	One " "	2000
Chondrodite (Humite), from Vesuvius	One " "	4000
Egyptian syenite (Cleopatra's Needle)	One " "	7000
Calcite	One " "	10,000
Natrolite	One " "	10,000
Ox bone	One " "	10,000
Meionite (Vesuvius)	One " "	10,000
Meteorite (Alfianello, Feb. 16, 1883)	One " "	100,000
Brevicite	One " "	200,000
Prehnite	One " "	500,000
Thomsonite	One " "	500,000
Vesbine, mixed with lava, from Vesuvius	One " "	700,000
Dolomite	One " "	1,000,000
Tobacco ash	One " "	1,000,000
Leucite, from Vesuvius	Less than one "	1,000,000
Nepheline, from Vesuvius	None	
Meteorite (Dhurmsala, 1860)	None	
Analcite	None	
Phenakite	None	
Chrysolite	None	
Haüynite	None	
Turquoise	None	

Indications of other spectrum-yielding elements.

89. Throughout the course of this paper I have devoted myself only to the citron-band spectrum. I do not, however, wish it to be thought that no other spectra were obtained. On the contrary, I have repeatedly seen indications of another very beautiful spectrum characterised by a strong red and a double orange band, and, more rarely, of a third spectrum distinct from the other two. These I am investigating, but not yet having obtained definite results I forbear from saying any more about them. I hope that they may bear sufficiently good fruit to be worthy of presentation at some future time to the Royal Society.

XXVIII. *On a new Crinoid from the Southern Sea.*

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Communicated by William B. Carpenter, *C.B., M.D., F.R.S.*

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[Plate 71.]

Towards the end of last year I received from Mr. Murray a small collection of "Challenger" *Comatulæ* which had been retained by the late Sir Wyville Thomson, and was found among his other collections after his death. It included several duplicates of forms already known to me, among them being three fairly perfect specimens of a type which I had only been able to study from a mutilated calyx. There were also eight or nine new species of *Antedon*, all from stations which had already yielded *Comatulæ*, two of them abundantly so. Lastly, there was an apparently insignificant little specimen from a depth of 1,800 fathoms at Station 158 in the Southern Sea.* It has five simple arms, and appeared at first sight to be merely a young individual of *Eudiocrinus semperi*,† which was dredged at Stations 164 and 169. Upon closer examination, however, I found that the specimen, although a true *Comatula*, and resembling *Eudiocrinus* in having but five arms, presents two characters which occur in no other Neocrinoid. In fact it is only among some of the older Palæocrinoids that similar features are to be met with, and I have no hesitation in saying that this is by far the most remarkable of all the Crinoids obtained by any of the recent deep-sea exploring expeditions.

Under these circumstances I propose to distinguish the type by the generic name *Thaumatocrinus*,‡ with the specific designation *renovatus*.

* Station 158, March 7, 1874, lat. 50° 1′ S., long. 123° 4′ E.; depth 1,800 fathoms; bottom temperature 3° C., Globigerina-ooze. The only other *Comatula* obtained at this station was *Promachocrinus abyssorum*.

† This is the *Ophiocrinus semperi* of my preliminary report (Proc. Roy. Soc., No. 194, 1879, p. 385). Owing to the previous employment of *Ophiocrinus* by Salter and also by Angelin, I have proposed *Eudiocrinus* for the recent type to which this name was given by Semper (Journ. Linn. Soc. Zool., vol. xvi., p. 493).

‡ *θαῦμα*, a marvel.

The total width of the calyx across the disc is barely 2 millims.; and the height of the centrodorsal and radials together is about the same. The former (Plate 71, figs. 1–4, *cd*) is rounded below, with its central canal completely closed up, so that it must have been detached for some little time from the remainder of the stem. The bases of half a dozen cirri are attached to it, and there are pits for the reception of two or three more. In the largest stump which is preserved (Plate 71, figs. 1, 3, *c*) the first two joints are quite short, as is usually the case, but the third reaches a length of 1·5 millim., so that the cirri must have been very like those of *Eudiocrinus semperi*. Except in this respect, however, and in the presence of five undivided arms, there is no further resemblance between the two types; for *Eudiocrinus* has a rosette, and consequently no basals appear externally. The radials are also only partially visible, owing to the extension of the centrodorsal over their lower surfaces, and the oral plates of the larva do not persist in the adult. But in *Thaumatocrinus* (Plate 71, figs. 1–4) there are relatively large basals (*b*), which completely separate the centrodorsal (*cd*) from the radials (*r*). This is itself an unusual feature in any *Comatula*, as will be explained further on.

Upon these five basals there rests a ring of ten arched plates, five of which (*r*) bear the arms, and are evidently the radials. But they *are not in contact laterally*, as is the case in every other five-rayed Neocrinoid with which I am acquainted, for they alternate with five smaller plates (*i*, *i*), which rest upon the truncated apices of the basals, while the radials rest in the angles formed by the adjacent sides of every two contiguous basals. Four of these five interradial plates terminate in a free edge at the margin of the disc; but the fifth, that on the anal side, bears a small tapering appendage of four or five joints, the last of which seems to end freely (Plate 71, figs. 2, 4, 5, *aa*).

The arms are composed of somewhat elongated joints, the second of which (Plate 71, figs. 1, 2, 4, b_2) bears the first pinnule. This is on the right side in three arms, and on the left in the other two. A similar variation occurs in *Eudiocrinus semperi*, but I do not attach much importance to it. The pinnules are very slender and delicate.

The disc resembles that of *Hyocrinus*. Its central portion is occupied by a relatively large oral pyramid (Plate 71, fig. 5, *o*), while between this and the margin are two or three irregular rows of small anambulacral plates (Plate 71, figs. 1–5, *an*), some of them extending up on to the lower part of the long anal tube (*at*). The large size and comparatively dense appearance of these orals indicates that they are not undergoing the process of resorption as those of other *Comatulæ* do. In some species (*e.g.*, *Ant. dentata*, Say = *A. sarsi*, Dub. and Kor.) the process is completed long before the end of the pentacrinoid stage; but in *Ant. rosacea* the orals persist in a partially resorbed condition after the loss of the stem, though they soon disappear completely.

Thaumatocrinus is thus the only *Comatula* yet known in which the oral plates of the larva persist, as they do in *Hyocrinus* and *Rhizocrinus*. The other peculiarities

which it exhibits are (1) the appearance of a closed ring of basals on the exterior of the calyx; (2) the separation of the radials by inter-radial plates; (3) the presence of a jointed arm-like appendage on the inter-radial of the anal side.

The persistence of the oral and basal plates of the larva, together with the small size of the specimen, might be thought to indicate that *Thaumatocrinus* is merely a type in which the resorption of the orals and the metamorphosis of the basals into a rosette take place unusually late. But as I have already pointed out, the condition of the centrodorsal, and of the cirri which it bears, is evidence that the specimen must have been detached from its stem for some little time, while the orals show no signs of any approaching resorption. The existence of the interradials also decidedly indicates that the basals on which they rest form a permanently closed ring on the exterior of the calyx. This is the case in but a very few *Comatulæ*, either recent or fossil.

Schlüter mentions a Cretaceous species in which it occurs;* while there are several forms, both of Cretaceous and of Jurassic age, in which the basal ring is incomplete, and the radials partly rest on the centrodorsal. But the only recent type in which the basals remain visible on the exterior of the calyx is the curious genus *Atelecrinus*;† and here they are very small in proportion to the radials. In all other recent *Comatulæ* the basals disappear from the exterior of the calyx towards the end of Pentacrinoid life, and become transformed into the rosette. Some species remain much longer in the Pentacrinoid stage than others; so that of two calices of equal size, the one may be still attached to a stem, the top joint of which bears but a few rudimentary cirri, and have large basals; while the other has a centrodorsal bearing 15 or 20 cirri, and concealing both the basals, and a part of the first radials. *Antedon rosacea* and *A. dentata* (*A. sarsi*, Dub. and Kor.) are two excellent instances of this difference, the latter attaining a length of 40 millims. in the Pentacrinoid state. A similar condition is presented by a Pentacrinoid which was dredged by the "Porcupine," and is probably to be referred to *Ant. eschrichti*, or to *Ant. quadrata*.‡ It is stouter and altogether more robust than any larva of *Ant. dentata* which I have seen; and though its radials are as large as those of the free *Thaumatocrinus*, yet its basals are actually higher than those of the single specimen of the latter type; while the centrodorsal on which they rest has merely a few imperfect cirrus-stumps, and is scarcely larger than the stem-joints below it. On the other hand, another larva from near Ascension (S. 344; 420 fathoms) has equally large radials resting directly on the centrodorsal, which bears about eight well-developed cirri; but the basals have already disappeared from the exterior of the calyx. An earlier stage in the development of this same larva is shown in Plate 71, fig. 6, for comparison with *Thaumatocrinus*. Although the calyx and arms are well developed, the basals (*b*)

* Zeitschr. d. Deutsch. Geol. Gesellsch., Jahrg. 1878, p. 66.

† Bull. Mus. Comp. Zoöl., vol. ix., No. 4, 1881, p. 16, pl. i., figs. 1–7.

‡ This is the *Ant. celtica* of Marenzeller, and of Duncan and Sladen; *non* Barrett.

separate the radials (*r*) from the centrodorsal (*cd*), which is, as yet, but slightly differentiated from the stemjoints below it. In all cases, however, the basals become concealed very soon after the conclusion of the Pentacrinoid stage, if not before. I can find no trace of them in various abyssal *Comatulæ*, which are no larger than *Thaumatocrinus renovatus*, and suspect therefore that in this type they persist through life as they do in *Atelecrinus*. Were they really only larval basals, and destined to have been eventually transformed into a "rosette," *Thaumatocrinus* would present a still more curious combination of characters than it actually does.

Both the persistence of the basals and the considerable development of the orals are characters which, either singly or combined, would cause the type to be regarded as one of no little interest; but they are altogether cast into the shade by the other peculiarities of the calyx, viz., the complete separation of the radials by relatively large interradial plates, and the presence of the anal appendage.

It might perhaps be suggested that the ten-rayed *Promachocrinus* affords some explanation of the first of these points. In this genus * the basals only exhibit a pentamerous symmetry, for the rosette into which they become transformed is connected with a basal star of five rays only, just as in any other *Comatula*. These five basal rays are attached to the dorsal surfaces of five out of the ten radials so as to partially separate them from the centrodorsal. These radials, therefore, are really interradial in position, and so correspond to the five interradial plates of *Thaumatocrinus*. But here the resemblance ceases; for the "interradial radials" of *Promachocrinus* precisely resemble the five true radials with which they alternate, and the arms borne by the two sets of plates are indistinguishable. I cannot, therefore, regard *Promachocrinus* as anything but a very regular variation of the usual pentamerous symmetry of the Crinoids.

Failing *Promachocrinus*, there is no other Neocrinoid which presents anything like the remarkable morphological condition of *Thaumatocrinus*. To find a corresponding developmental stage we must go back to a very early period in the ontogeny of a Crinoid, *i.e.*, one but little later than the appearance of the rudiments of the lowest arm-plates. The radials first appear as isolated plates in the spaces "where the upturned angles of two oral plates are opposed to the bevelled off upper angles of two adjacent basals."† They gradually increase in size, and ere long come to form a nearly complete circle, two of them being separated for a time by the anal plate. This is eventually lifted out from between them, but the radials of *Ant. rosacea* do not come into complete lateral contact until after the appearance of the first whorl of cirri. In the larva represented in Plate 71, fig. 6, however, the cirri do not appear until the radials have met laterally, and the arm-bases are well developed. The radials of a mature *Comatula*, therefore, form a closed ring of five plates; and any interradials which may subsequently appear are limited to the angles between adjacent second

* Proc. R. S., No. 194, 1879, p. 385; see also Journ. Linn. Soc. Zool., vol. xv., p. 214, pl. 12, fig. 28.

† C. Wyville Thomson, "On the Embryogeny of *Antedon rosaceus*," Phil. Trans., 1865, p. 528.

and third radials, though sometimes attaining a considerable relative size and importance, as in *Guettardicrinus* and some species of *Apiocrinus*.

It is well known that many peculiarities which are merely transitory in young larvæ of the Neocrinoids, are permanently retained in some of the Palæocrinoids. This is the case, for example, with the primitive position of the anal plate within the ring of (first) radials of the larval *Antedon*. Thus in the Devonian genus *Hexacrinus* (Austin), and in some allied forms from the Carboniferous limestone among the *Platycrinidæ*, two of the five radials are separated permanently by a single large anal plate; and the still earlier condition, before the radials have come into lateral contact at all, finds a parallel in the remarkable genus *Reteocrinus*,* from the Trenton and Hudson River groups (Lower Silurian) of North America. In this type, however, the radials are separated by what Messrs. Wachsmuth and Springer† describe as an "interradial series resting directly upon the basals, consisting of a very large number of minute pieces of irregular form, and without definite arrangement." A similar development of small irregular plates between the rays occurs in many Neocrinoids, both stalked and free, but the interradial series always commence at the level of the second or third radials, and are completely separated from the basals by the ring of united first radials.

Now in *Thaumatocrinus* we not only find the primitive lateral separation of the radials to be permanent, as in *Reteocrinus*, but instead of the small and irregular interradials which rest on the basals of that type, *Thaumatocrinus* has one relatively large plate between every two radials (Plate 71, figs. 1–4, *i*, *i*). This is, as it were, a further development of the embryonic condition, but in a new direction. It is, however, one which is not to be found in any Neocrinoid, either recent or fossil, and it is only among certain of the Palæozoic *Rhodocrinidæ* that a similar peculiarity presents itself. Messrs. Wachsmuth and Springer have grouped the genera in which it occurs into a special section, *Rhodocrinites*.‡ They are *Lyriocrinus* (Hall); *Rhipidocrinus* (Beyrich); *Thylacocrinus* (Oehlert); *Anthemocrinus* (W. and S.); *Rhodocrinus* (Miller); and *Ollacrinus* (Cumberland). All of them have a ring of ten plates resting on the basals, viz., the radials and five interradials of about the same size. This is well shown in the diagram of the calyx of *Thylacocrinus* (Plate 71, fig. 7), which I have copied from that given by Oehlert.§

While resembling the *Rhodocrinites* in having five large plates separating the radials, *Thaumatocrinus* differs from them, and from most Palæocrinoids, in the absence of any higher series of calicular interradial plates resting upon the first series which

* Of Billings, *emend.* Wachsmuth and Springer.

† "Revision of the Palæocrinoidea," Part II., p. 192. From the Proceedings of the Philadelphia Academy, July 26, 1881, p. 366.

‡ *Ibid.*, pp. 182–184.

§ "Description de deux nouveaux genres de Crinoïdes du terrain dévonien de la Mayenne." Bull. Soc. Géol. de France. 3e Ser., Tom. vii., pl. 1., fig. 2.

separate the radials. Except on the anal side, these primary interradial plates of *Thaumatocrinus* end simply in a free rounded edge at the margin of the disc (Plate 71, figs. 1–3, 5, i), which is doubtless due to the simplicity of the arms; for these become free almost at once, and are not connected laterally by much perisome, in which higher orders of interradials could be supported. But in the presence of the appendage on the azygous interradial (Plate 71, figs. 2, 4, 5, *aa*), *Thaumatocrinus* bears a remarkable resemblance to *Reteocrinus*. The latter genus was established by BILLINGS on some badly preserved fragments from the Trenton limestone of Ottawa.* MEEK, and WETHERBY have since described some species of *Glyptocrinus* presenting very similar characters to those of BILLINGS' genus, and have noted the resemblance between them; while WETHERBY† subsequently came to the conclusion "that several forms of our so-called *Glyptocrinus* should be referred to this genus." WACHSMUTH and SPRINGER‡ have accordingly reconstructed *Reteocrinus*, and have proposed as type of the genus *Glyptocrinus nealli* (HALL), a proceeding for which they have been severely criticised by MILLER.§

The original examples of BILLINGS' type species were so imperfectly preserved, that the distinctive characters of his genus were incompletely known. As, however, WACHSMUTH and SPRINGER, like WETHERBY, fully believed *Glyptocrinus nealli* to be a *Reteocrinus*, I do not see how they could have redefined the genus better than by selecting such a well-known species as their type.

Taking *Reteocrinus* then as defined by WACHSMUTH and SPRINGER, we find that its posterior interradial area is wider than the other four, "with a conspicuous row of decidedly larger and more prominent special anal plates along the median part." BILLINGS gives a good figure of this structure in *R. stellaris*,‖ and speaks of it as follows: "If this series of joints constitute a true arm, then there must be six arms in this species." The same feature appears, though less prominently, in *R. nealli* (HALL) sp., and in *R. baeri* (MEEK) sp., and also in *R. richardsoni* (WETHERBY), though in *R. gracilis* (WETHERBY) and *R. cognatus* (MILLER) sp., it appears to be absent. It is unusually distinct, however, in *Xenocrinus penicillus* (MILLER)¶ (Plate 71, fig. 8), a type which closely resembles *Reteocrinus* in general appearance; and I fully agree with Messrs. WACHSMUTH and SPRINGER** in thinking that it should

* 'Canadian Organic Remains.' Decade iv., p. 63.

† "Description of new Fossils from the Lower Silurian and Subcarboniferous Rocks of Ohio and Kentucky." Journ. Cincinnati Soc. Nat. Hist., vol. iv., April, 1881, p. 7 (of separate copy).

‡ Revision. II., p. 191.

§ "Description of Two New Genera and Eight New Species of Fossils from the Hudson River Group." Journ. Cincinnati Soc. Nat. Hist., vol. v., April, 1882, pp. 12, 13 (of separate copy).

‖ *Op. cit.*, p. 64, pl. 9, fig. 4*a*.

¶ "Description of Some New and Remarkable Crinoids and other Fossils of the Hudson River Group, and notice of *Strotocrinus bloomfieldensis*." Journ. Cincinnati Soc. Nat. Hist., vol. iv., April, 1881, pl. 1, fig. 3, and pl. 4, fig. 4, pp. 71–73.

** Revision. II., p. 185.

be associated with the *Rhodocrinidæ* rather than with the *Actinocrinidæ* to some of which (*e.g.*, *Melocrinus*) it would be allied, owing to the presence of a tetramerous base. Wachsmuth and Springer point out that "no Actinocrinoid has ever been discovered in which the interradial field, except at the azygous side, extends to the basal disc." But Miller's description, which is borne out by his figures (one of which is reproduced in Plate 71, fig. 8), runs as follows: "The azygous area is remarkably large, and covered in the central part by a vertical series of plates having about the same size as the regular radial series, and upon each side of the vertical series there is a depressed area covered by small plates having a tubercle in the central part, as in the regular interradial areas. There are seven plates, each having a length about twice as great as its width, in the vertical series, from the basal plate upon which the series rests to the top of the vault. This vertical series is continued to the top of the proboscis, and contains in its entire length more than fourteen plates. It has such strong resemblance to the radial series, except as to the branching at the secondary radials, that the general appearance of the body is that of a species having six radial series."

There can, I think, be no reasonable doubt that the anal appendage of *Thaumatocrinus*, although free laterally, owing to the simplicity of the rays, is homologous with the vertical series of plates in the anal interradius of *Reteocrinus* and *Xenocrinus*; and it is not a little curious to find a character which died out some time before the Mesozoic epoch recurring in a recent *Comatula*. I am quite at a loss as to the probable function of this anal appendage in *Thaumatocrinus*, but it seems to differ from that of the Palæocrinoids in one point, for Miller describes it in *Xenocrinus* as continued to the top of the proboscis, which is not the case in *Thaumatocrinus*. The lower part of the anal tube bears plates, but they are continuous with those covering the disc over which the anal appendage arches, without, however, forming any connexion with the plates in question.

It is difficult to consider the existence of interradials and of the anal appendage of *Thaumatocrinus* as instances of atavism, for no known Neocrinoid presents any similar characters, and it is a long way back from a recent *Comatula* to a Palæozoic Crinoid. The appendage soon disappeared, both the genera possessing it being of Lower Silurian age; but Crinoids with the interradials resting on the basals persisted into the Carboniferous period, and possibly also some with an anal appendage. Nothing of the kind is visible, however, in any genus of Neocrinoids, so that the reappearance of these characters in such a specialised type as a *Comatula* is not a little surprising. Associated with them we find the distinctly embryonic characters of persistent basal and oral plates, the latter occurring in no other *Comatula*, together with the simplicity of the undivided arms.

Thaumatocrinus is thus a type of unusual interest, and should be sought for carefully in any future deep-sea explorations. It is evident that the possibilities of the abyssal fauna are by no means exhausted yet.

The presence of the oral pyramid in *Thaumatocrinus*, as in *Hyocrinus*, suggests the

idea that the little specimen obtained from a depth of 2,325 fathoms, at Station 223 in the east Pacific, may, perhaps, be related to the former genus. Sir WYVILLE THOMSON* spoke of it as *Hyocrinus bethellianus* (?), with the remark, "It is certainly in many respects very unlike the adult *H. bethellianus*, but it may possibly turn out to be the young of that species." No figure of it is to be found either in the "Atlantic" or in any of the numerous plates which were drawn at Edinburgh under Sir WYVILLE'S direction, and it is to be feared that this "beautiful little thing" has been mislaid, as Mr. MURRAY has been unable to discover it among the material which was in Sir WYVILLE'S hands at the time of his death.

The discovery of *Thaumatocrinus* restores the numerical equality between the living genera of *Comatulæ* and of stalked Crinoids, and raises their joint total to twelve. Species of every genus, except *Holopus*, have been obtained by the various British expeditions for deep-sea exploration, as shown in the following table:—

Family.	Genera.	Number of species obtained.	Remarks.
Comatulidæ	*Antedon*, FREM.	83	Seven obtained by the "Porcupine" and the "Triton." The rest by the "Challenger."
	Actinometra, MÜLL.	52	"Challenger." One by the ["Porcupine."
	Promachocrinus, P.H.C.	3	"
	Eudiocrinus, P.H.C.	3	"
	Atelecrinus, P.H.C.	2	"
	Thaumatocrinus, P.H.C.	1	"
Pentacrinidæ	*Pentacrinus*, MILLER	5	One obtained by the "Porcupine;" one species doubtful, perhaps representing a new genus.
	Metacrinus WY. TH., and P.H.C.	10	One founded on stem fragments only.
Bourgueticrinidæ	*Rhizocrinus*, SARS.	2	"Challenger" and "Porcupine."
	Bathycrinus, WY. TH.	3	One obtained by the "Porcupine."
Hyocrinidæ	*Hyocrinus*, WY. TH.	1	Besides one doubtful young specimen.

General considerations.

The peculiarities of *Reteocrinus*, as well as of *Thaumatocrinus*, have suggested certain morphological considerations bearing on the various classifications of the *Rhodocrinidæ* that have hitherto been proposed.

One cannot help wondering where the circular commissure of *Reteocrinus* was situated. In ordinary Crinoids with directly contiguous radials, each of them is traversed by a portion of the circular canal in which the commissure is lodged. But

* "Notice of New Living Crinoids belonging to the *Apiocrinidæ*." Journ. Linn. Soc. Zool., vol. xiii., p. 55.

in *Reteocrinus* and in *Xenocrinus* (Plate 71, fig. 8) the isolated radials are quite narrow, and the interradial spaces separating them are sometimes twice their breadth. How did the circular commissure traverse these spaces? Whether there were canals in the radials or not, the interradial portions of the commissures must have been freely exposed to the body-cavity at the bottom of the calyx, for it is not likely either that the commissure was absent, or that it was situated within the ring of basal plates. In this respect also, therefore, *Reteocrinus* presents an embryonic feature, for in the earlier stages of Pentacrinoid life the axial cords simply lie on the ventral surface of the radials and brachials, without having any channels hollowed out in these plates for their reception, as is subsequently the case; and whatever was the case with the radials and basals of *Reteocrinus*, it is improbable that the irregular interradial plates which were crossed by the cords were in any way grooved for their reception.* These may fairly be regarded as corresponding to the numerous irregular plates which occur upon the disc and between the rays of many Neocrinoids. Those of *Reteocrinus*, however, do not stop at the level of the second radials, but extend right down to meet the basals. Sometimes there appear to be only one or two between every two radials, *e.g.*, *R. gracilis*, but in other cases the number seems to be larger, and the plates can hardly be regarded as the complete morphological equivalents of the larger and more regular single interradials which occur in the *Rhodocrinidæ*.

The interradial portions of the circular commissure must have passed over the ventral surface of these large plates, if not actually piercing them. The same must be the case in *Thaumatocrinus*, and unless its radials are different from those of all other Neocrinoids, the axial cords must be lodged in canals, which is probably also true for the interradials. In any case, however, the relation of these plates to the axial cords shows that they belong, like the radials and basals, to the radial system, rather than to the perisomatic. It is not easy to make out their homologies in other Echinoderms, but they are perhaps represented in the disc of an Ophiurid by the proximal row of intermediate plates, while the interradials generally correspond to the distal rows.

The morphological differences involved in the separation or lateral union of the

* Müller, and more recently Zittel, have considered the presence or absence of canals within the calyx-plates as affording an important character which distinguishes the Palæozoic from the younger Crinoids. There are many Palæocrinoids, however, in which these canals are present, *e.g.*, *Allagecrinus*, *Platycrinus*, and all forms with true articular facets on the distal faces of the radials. *Platycrinus* has, nevertheless, been placed by Professor Chapman in his division *Emedullata*, the calyx and arm-plates of which are "without internal canals" (See "A Classification of Crinoids," read before the Royal Society of Canada, May 26, 1882). Strangely enough, *Marsupites* is placed in the same division, although any specimen with a good articular surface on the radials shows the opening of the central canal as distinctly as possible, and the canal actually pierces the substance of the plate, not ending abruptly on its ventral surface, as in the radials of *Cupressocrinus*.

(first) radials seem to have been first noticed by Zittel.* For he made them a fundamental distinction between the two families of *Glyptocrinidæ* and *Rhodocrinidæ*, in which he placed several genera that had been somewhat scattered in previous classifications. To the latter he referred types with a more or less depressed or spherical calyx, in which the lowest interradials rest directly on the basals, and form, together with the radials, a ring of ten alternating plates, *e.g.*, *Rhodocrinus* and *Ollacrinus*. In the *Glyptocrinidæ*, on the other hand, the calyx is higher, and the lowest interradials rest upon the upper edges of contiguous radials. This family includes *Glyptocrinus* and *Glyptaster* (Hall), with *Eucrinus* (Angelin), and also *Thylacocrinus* (Oehlert), which seems somewhat out of place; for it has a large globular calyx, and five large interradials, which completely separate the radials from one another (Plate 71, fig. 7).

Messrs. Wachsmuth and Springer† express considerable doubt whether the differences between these two families in Zittel's classification, "even if they were persistent, can be deemed sufficient for a family distinction. *Thysanocrinus* of the *Rhodocrinidæ* has generally at four sides the first interradial disposed between the first and second radials; while in *Thylacocrinus*, according to Oehlert's figure (Plate 71, fig. 7), all five first interradials rest directly upon the basals." I must confess that I cannot quite follow this argument. The *Thysanocrinus* referred to is Hall's type of that name, which Wachsmuth and Springer subsequently place under *Dimerocrinus* (Phillips); and in their generic diagnosis of it they say, "Interradial areæ composed of but few plates, the first one large, placed between the second radials, and leaning partly against the third, with two small plates above. Posterior, or anal area wider, the first plate in line with the first radials, and of the same size." *Thylacocrinus*, on the other hand, is said to have "Interradials numerous, the lower one resting directly on the basals;" *i.e.*, all five interradials meet the basals, and not that on the anal side only. This difference is further recognised by Wachsmuth and Springer, for they place the two genera in different sections of their family *Rhodocrinidæ*; and I do not, therefore, see the force of their doubts respecting the persistency of the characters in this portion of Zittel's classification. In fact, they make great use of the position of the lowest interradials in defining their subdivisions of the family.

According to their general description of the *Rhodocrinidæ*, "In most of the genera the first interradial rests directly upon the truncate upper side of the basals, thereby separating the first radials all round. In others, however, only the first plate of the posterior or anal side is supported by a basal, that of the other four sides being placed against the upper corners of the first, and between the second radials, the former producing an almost pentahedral, the latter a more or less bilateral symmetry." This

* 'Palæontologie,' pp. 374–376.

† Revision. II., pp. 181, 182.

is perfectly true, and the distinction sharply marks off the section of bilateral *Glyptasterites* from the pentahedral *Rhodocrinites*.

The section *Glyptocrinites*, however, is somewhat heterogeneous. Its calyx is said to be almost perfectly pentahedral with the "interradial areas depressed, the first plate resting either directly upon the basals, or between the second and third radials, without special anal plate beneath their line." Only three genera are included in this section, and Messrs. WACHSMUTH and SPRINGER seem to have been somewhat uncertain about so grouping them; for they remark (p. 183), "It might have been not out of the way if we had placed the genus *Glyptocrinus* in a group by itself, as it differs from *Archæocrinus* and *Reteocrinus*, with which it has been associated, *and from all other Rhodocrinidæ*,* in having the first plate at each interradial side placed between the second radials."

In *Archæocrinus* (W. and S.), on the other hand, the lowest interradials rest directly upon the basals, as is also the case with the small and irregular interradials of *Reteocrinus*. Both these genera, therefore, have isolated radials and a pentahedral symmetry ("somewhat bilateral" in *Reteocrinus*) just as in the *Rhodocrinites*. But the latter lack the "rounded strongly elevated ridges" which distinguish the radials of *Archæocrinus* and *Reteocrinus*. This, however, is merely a character in the superficial ornamentation of the calyx; and it seems to me of altogether minor importance as compared with the morphological differences between the lateral union and the isolation of the radials. In this last feature *Archæocrinus* and *Reteocrinus* resemble the *Rhodocrinites*, and if the limits of that section could not be enlarged to receive them, they might very well be left in a group by themselves, distinguished by their ornamentation.

But they are out of place by the side of *Glyptocrinus*, with *all* its radials united laterally. It thus represents a comparatively late ontogenetic condition, not even the radials of the posterior side being separated by an anal plate as in the *Glyptasterites*. There are, doubtless, close affinities and remarkable transition forms between *Glyptocrinus* and *Reteocrinus*, as asserted by Messrs. WACHSMUTH and SPRINGER. But these depend very largely upon the characters of the rays and arms, which are of a comparatively subordinate value; while the lateral separation of the radials in the last named genus, and in the *Rhodocrinites*, is a fact of considerable importance in Crinoid Morphology.

It must be remembered also that *Glyptocrinus* has decided affinities with some of the earlier *Actinocrinidæ*, certain species appearing to be without under-basals. In fact, according to the American authors, "It is a question whether that genus, at least partly, should not be arranged with the other group altogether."

Thus, then, I would divide the *Rhodocrinidæ* (W. and S.) into groups as follows:—

* The italics are mine.

I. Radials completely separated laterally, either by single interradial plates, or by groups of small ones.	
α. No ridges on the radials	*Rhodocrinites* (W. and S.)
β. With ridges on the radials	*Archæocrinus.* / *Reteocrinus.*
II. The two posterior radials separated by an anal plate which rests on a basal	*Glyptasterites* (W. and S.)
III. Radials in contact all round the calyx	*Glyptocrinus.*

I cannot help suspecting, however, that ZITTEL's arrangement of these genera into two families, *Glyptocrinidæ* and *Rhodocrinidæ*, is the most natural one; though I should place *Thylacocrinus* in the latter, and not in the former as he has done.

POSTSCRIPT.

(Added February 1, 1884.)

During the past year the peculiarities of *Thaumatocrinus* have naturally been much in my mind, and I have been led to believe that the structure which I have called the anal appendage is represented in other Palæocrinoids besides the two Silurian genera already mentioned.

WACHSMUTH and SPRINGER* describe *Taxocrinus* and *Onychocrinus* as having a small lateral proboscis in the anal area, which consists of a series of from two to six narrow quadrangular plates, longitudinally arranged, and resting on the upper surface of a basal. MEEK and WORTHEN† spoke of it in *Onychocrinus* as "really looking very much like a diminutive arm rising from the anal area;" and they subsequently found the remainder of the anal interradius to be occupied by a great number of minute irregular plates, which pass gradually upwards into those of the "vault," just as in *Reteocrinus* and *Xenocrinus*. If *Thaumatocrinus* were a larger type, with plated perisome between the rays, as in *Pentacrinus asteria*, its tapering anal appendage would be in the same condition as that of *Onychocrinus*, becoming merged above into the general plating of the anal interradius.

I do not think, therefore, that WACHSMUTH and SPRINGER are quite correct in describing *Taxocrinus* and *Onychocrinus* as having "a small lateral tube." That the arm-like series of plates supported the lower portion of the anal interradius is doubtless true. But I do not imagine the plates to have been in any way hollowed on their inner sides for the reception of the hind-gut. This undoubtedly opened to the exterior at a higher level, through a regular anal tube just as in other Crinoids.

* Revision. I., pp. 46–53.

† 'Palæontology of Illinois,' vol. ii., p. 243; vol. iii., p. 494.

Excellent figures of the anal series in *Taxocrinus* are given by SCHULTZE* and ANGELIN,† while that of *Onychocrinus* is well represented by MEEK and WORTHEN.‡ These figures may be advantageously compared with those of *Thaumatocrinus* on Plate 71.

Since the preceding paper was presented to the Society in April, 1883, the discussion between Messrs. MILLER and WACHSMUTH respecting the nature of *Reteocrinus* has been carried on with considerable vigour.

Stimulated by MILLER's criticisms, Messrs. WACHSMUTH and SPRINGER were able (with the help of Mr. W. R. BILLINGS) to demonstrate a considerable amount of resemblance between *Reteocrinus stellaris* (BILLINGS), and *Glyptocrinus nealli* (HALL). Both types have (1) the under-basals visible externally, (2) the radials separated laterally by the lowest interradials, which rest on the basals, and (3) a prominent median row of plates in the anal interradius; though WACHSMUTH and SPRINGER do not lay much stress upon the last point. "*Reteocrinus* is readily identified by its highly elevated radial ridges, and depressed interradial spaces, filled with numerous small plates of irregular arrangement, and extending between the first radials down to the basals; by its under-basals, often well developed; its strongly marked bilateral symmetry; and by its ten primary arms as a rule."§

MILLER replied by giving a detailed comparison of *Glyptocrinus nealli* and *Reteocrinus stellaris*, and believed himself to have found such great differences between them, "that it is doubtful whether they should even be classified in the same family."‖ He lays much stress upon differences in the general aspect of the cup and arms; a little more so, perhaps, than is necessary, considering the poor state of preservation of the Canadian specimens. Two points, however, seem to me to be of greater importance. In all the species which have been lately referred to *Reteocrinus* by WACHSMUTH and SPRINGER, the under-basals are poorly developed, or perhaps even absent; while the third radial is the axillary. But in *R. stellaris* there are quite large under-basals, and the fourth radial is the axillary; and I have some doubt, therefore, as to the advisability of referring to this little-known generic type a number of species which do not present these characters, more especially the latter one. They all agree, however, with *Reteocrinus stellaris* in a feature which both WACHSMUTH and SPRINGER and I myself regard as specially distinguishing *Reteocrinus* from *Glyptocrinus*, viz.,

* "Monographie der Echinodermen des Eiflerkalkes." Denkschr. d. Wiener Akad. Bd. xxvi., 1866. Taf. iv., figs. 2, 2*b*, 3, 4*b*.

† "Iconographia Crinoideorum," &c. Stockholm, 1878. Tab. xviii., fig. 8. Tab. xx., figs. 9, 13, 16. Tab. xxiii., fig. 5.

‡ 'Palæontology of Illinois,' vol. v., pl. xiv., fig. 4.

§ "Remarks on *Glyptocrinus* and *Reteocrinus*, two genera of Silurian Crinoids." Amer. Journ. Sci., vol. xxv., April, 1883, pp. 265-266.

‖ "Response to the Remarks of Messrs. WACHSMUTH and SPRINGER on the genera *Glyptocrinus* and *Reteocrinus*." Amer. Journ. Sci., August, 1883, p. 112.

the separation of the first radials by the calyx-interradials. WALCOTT* has recently pointed out that a new species, which he has described as possessing this character, "departs from the typical form of *Glyptocrinus*," and he suggests its reference to another generic type. MILLER, however, regards this striking difference in the position of the lowest interradial as of no systematic value whatever, even for specific classification. For he identifies *Reteocrinus gracilis* (WETHERBY), with a type previously described by himself as *Glyptocrinus angularis*, and since recognised by WACHSMUTH as a true *Glyptocrinus*. The lowest interradials rest "between the upper sloping sides of the first radials;" while in *R. gracilis* the radials are widely separated laterally, and the lowest plates of the irregular interradial series rest upon the basals. This feature also occurs in four species which are referred by MILLER† to *Glyptocrinus*, although in *G. decadactylus*, which he takes as his type, "the regular interradial areas have one plate resting upon the primary radials!"

But MILLER goes even further than this. He establishes a new genus, *Gaurocrinus*, for types hitherto described under *Glyptocrinus*, but possessing a dicyclic base; and he refers to it five species, two of which are new. In one of these, and in the three species previously known, the lowest interradials rest upon the basals. But in *Gaurocrinus splendens*, n.sp., the large hexagonal basals are "not truncated upon the upper face by an interradial." MILLER'S mode of classification, therefore, totally disregards such important morphological differences as the separation or lateral union of the primary radials; and I cannot believe that it will find acceptance among philosophical palæontologists.

Gaurocrinus differs from *Glyptocrinus* in having a dicyclic base,‡ that of *Glyptocrinus*

* "Descriptions of new species of Fossils, from the Trenton Group of New York." 35th Ann. Report N. Y. State Mus. Nat. Hist., p. 2 (of separate copy).

† "*Glyptocrinus* redefined and restricted, *Gaurocrinus Pycnocrinus*, and *Compsocrinus* established." Journ. Cincinn. Soc. Nat. Hist., Dec., 1883, vol. vi., pp. 217-228.

‡ It is much to be regretted that Mr. MILLER still uses the empirical and utterly irrational nomenclature, which is now being gradually replaced by a system based upon sound morphological considerations. He remarks that "the policy of changing the nomenclature may well be doubted, and ought not to be entered upon without the clearest conviction that, by so doing, error of some kind is being eradicated." No better illustration of such an error could be found than his statement that *Gaurocrinus* "is primarily distinguished from *Glyptocrinus* by possessing five sub-radials." This name was given by DE KONINCK to the so-called parabasals of MÜLLER, "afin de faire comprendre qu'ils alternent avec les radiales;" and since "the presence or absence of sub-radial plates is regarded of special generic importance" by Mr. MILLER, we are led to conclude that the "basals" of *Glyptocrinus* (MILLER), in which sub-radials are absent, do *not* alternate with the radials. But this is exactly contrary to the fact! Sub-radial plates, alternating with the radials, *are invariably present;* and it is the radially situated under-basals which may be "present or absent." In the former case Mr. MILLER calls them basals, which name he also gives to the sub-radial plates when there are no under-basals.

This method is doubtless both "easy" and "expressive." But it unfortunately implies an homology between the radially situated plates of one genus (*e.g.*, *Poteriocrinus*), and plates which are interradial in another (*e.g.*, *Platycrinus*); and this is utterly opposed to the fundamental principles of morphology, not only in the Crinoids, but also in the Echinoderms generally.

being monocyclic only. It is curious, however, that MILLER should make *Glyptocrinus decadactylus* the type of a genus, the speciality of which is the presence of a monocyclic base. For HALL, MEEK, and WACHSMUTH* have all described it as being dicyclic, *i.e.*, as possessing under-basals.

It has been abundantly proved within the last few years that the presence or absence of under-basals upon the exterior of the calyx is a character which is generally of very little value for systematic purposes. *Encrinus* and *Heterocrinus* afford good instances of this. The late Mr. MEEK, whose judgment Mr. MILLER will hardly question, was fully aware of the great amount of variation in the cup of *Heterocrinus*, some species having one series of plates beneath the radials, and others, two; while he further recognised that the upper row of the dicyclic base represents the single row of the monocyclic forms.

The same is the case with *Glyptocrinus* and its allies, as was recognised by WACHSMUTH and SPRINGER, though MILLER will not admit it. One would like to know whether he would rearrange the species of *Heterocrinus* on the principles which have led him to separate *Gaurocrinus* from *Glyptocrinus*.

DESCRIPTION OF THE FIGURES.

PLATE 71.

The following lettering is used throughout all the figures:—*aa*, anal appendage; *an*, anambulacral plates; *at*, anal tube; *b*, basals; b_2, second brachial; *c*, cirrus; *cd*, centrodorsal; *i*, interradial plates; *o*, orals; *r*, radials.

Figs. 1–5.—*Thaumatocrinus renovatus*. All × 15.

Figs. 1 and 2. Side views, radial. In 1, the right anterior, and in 2, the right posterior ray faces the observer.

Figs. 3 and 4. Side views, interradial. Fig. 3 shows the left anterior interradius with its single large interradial (*i*) and anambulacral plates (*an*).

Fig. 4 shows the posterior or anal interradius, in which the interradial plate bears the jointed anal appendage (*aa*).

Fig. 5. View of the disc from above, showing the anal tube and appendage, the oral pyramid, and the marginal zone of anambulacral plates.

Fig. 6. Radial view of an *Antedon*-Pentacrinoid from S. 344, showing the lateral union of the radials. × 15.

Fig. 7. Calyx of *Thylacocrinus*; after OEHLERT.

Fig. 8. Anal side of *Xenocrinus penicillus*, showing the anal appendage (*aa*); after MILLER.

* Revision. II., p. 7.

XXIX. *An Experimental Investigation of the Circumstances which determine whether the Motion of Water shall be Direct or Sinuous, and of the Law of Resistance in Parallel Channels.*

By Osborne Reynolds, *F.R.S.*

Received and Read March 15, 1883.

[Plates 72–74.]

Section I.

Introductory.

1. *Objects and results of the investigation.*—The results of this investigation have both a practical and a philosophical aspect.

In their practical aspect they relate to the *law of resistance to the motion of water in pipes*, which appears in a new form, the law for all velocities and all diameters being represented by an equation of two terms.

In their philosophical aspect these results relate to the fundamental principles of fluid motion; inasmuch as they afford for the case of pipes a definite verification of two principles, which are—*that the general character of the motion of fluids in contact with solid surfaces depends on the relation between a physical constant of the fluid and the product of the linear dimensions of the space occupied by the fluid and the velocity.*

The results as viewed in their philosophical aspect were the primary object of the investigation.

As regards the practical aspect of the results it is not necessary to say anything by way of introduction; but in order to render the philosophical scope and purpose of the investigation intelligible it is necessary to describe shortly the line of reasoning which determined the order of investigation.

2. *The leading features of the motion of actual fluids.*—Although in most ways the exact manner in which water moves is difficult to perceive and still more difficult to define, as are also the forces attending such motion, certain general features both of the forces and motions stand prominently forth, as if to invite or to defy theoretical treatment.

The relations between the resistance encountered by, and the velocity of, a solid body moving steadily through a fluid in which it is completely immersed, or of water

moving through a tube, present themselves mostly in one or other of two simple forms. The resistance is generally proportional to the square of the velocity, and when this is not the case it takes a simpler form and is proportional to the velocity.

Again, the internal motion of water assumes one or other of two broadly distinguishable forms—either the elements of the fluid follow one another along lines of motion which lead in the most direct manner to their destination, or they eddy about in sinuous paths the most indirect possible.

The transparency or the uniform opacity of most fluids renders it impossible to see the internal motion, so that, broadly distinct as are the two classes (direct and sinuous) of motion, their existence would not have been perceived were it not that the surface of water, where otherwise undisturbed, indicates the nature of the motion beneath. A clear surface of moving water has two appearances, the one like that of *plate glass*, in which objects are reflected without distortion, the other like that of *sheet glass*, in which the reflected objects appear crumpled up and grimacing. These two characters of surface correspond to the two characters of motion. This may be shown by adding a few streaks of highly coloured water to the clear moving water. Then although the coloured streaks may at first be irregular, they will, if there are no eddies, soon be drawn out into even colour bands; whereas if there are eddies they will be curled and whirled about in the manner so familiar with smoke.

3. *Connexion between the leading features of fluid motion.*—These leading features of fluid motion are well known and are supposed to be more or less connected, but it does not appear that hitherto any very determined efforts have been made to trace a definite connexion between them, or to trace the characteristics of the circumstances under which they are generally presented. Certain circumstances have been definitely associated with the particular laws of force. Resistance, as the square of the velocity, is associated with motion in tubes of more than capillary dimensions, and with the motion of bodies through the water at more than insensibly small velocities, while resistance as the velocity is associated with capillary tubes and small velocities.

The equations of hydrodynamics, although they are applicable to *direct motion*, *i.e.*, without eddies, and show that then the resistance is as the velocity, have hitherto thrown no light on the circumstances on which such motion depends. And although of late years these equations have been applied to the theory of the eddy, they have not been in the least applied to the motion of water which is a mass of eddies, *i.e.*, in *sinuous motion*, nor have they yielded a clue to the cause of resistance varying as the square of the velocity. Thus, while as applied to waves and the motion of water in capillary tubes the theoretical results agree with the experimental, the theory of hydrodynamics has so far failed to afford the slightest hint why it should explain these phenomena, and signally fail to explain the law of resistance encountered by large bodies moving at sensibly high velocities through water, or that of water in sensibly large pipes.

This accidental fitness of the theory to explain certain phenomena while entirely

failing to explain others, affords strong presumption that there are some fundamental principles of fluid motion of which due account has not been taken in the theory. And several years ago it seemed to me that a careful examination as to the connexion between these four leading features, together with the circumstances on which they severally depend, was the most likely means of finding the clue to the principles overlooked.

4. *Space and velocity.*—The definite association of resistance as the square of the velocity with sensibly large tubes and high velocities, and of resistance as the velocity with capillary tubes and slow velocities seemed to be evidence of the very general and important influence of some properties of fluids not recognised in the theory of hydrodynamics.

As there is no such thing as absolute space or absolute time recognised in mechanical philosophy, to suppose that the character of motion of fluids in any way depended on absolute size or absolute velocity, would be to suppose such motion without the pale of the laws of motion. If then fluids in their motions are subject to these laws, what appears to be the dependance of the character of the motion on the absolute size of the tube and on the absolute velocity of the immersed body, must in reality be a dependance on the size of the tube as compared with the size of some other object, and on the velocity of the body as compared with some other velocity. What is the standard object and what the standard velocity which come into comparison with the size of the tube and the velocity of an immersed body, are questions to which the answers were not obvious. Answers, however, were found in the discovery of a circumstance on which sinuous motion depends.

5. *The effect of viscosity on the character of fluid motion.*—The small evidence which clear water shows as to the existences of internal eddies, not less than the difficulty of estimating the viscous nature of the fluid, appears to have hitherto obscured the very important circumstance that *the more viscous a fluid is, the less prone is it to eddying or sinuous motion.* To express this definitely—if μ is the viscosity and ρ the density of the fluid—for water $\frac{\mu}{\rho}$ diminishes rapidly as the temperature rises, thus at 5° C. $\frac{\mu}{\rho}$ is double what it is at 45° C. What I observed was that the tendency of water to eddy becomes much greater as the temperature rises.

Hence connecting the change in the law of resistance with the birth and development of eddies, this discovery limited further search for the standard distance and standard velocity to the physical properties of the fluid. To follow the line of this search would be to enter upon a molecular theory of liquids, and this is beyond my present purpose. It is sufficient here to notice the well known fact that

$$\frac{\mu}{\rho} \text{ or } \mu'$$

is a quantity of the nature of the product of a distance and a velocity.

It is always difficult to trace the dependance of one idea on another. But it may be noticed that no idea of dimensional properties as indicated by the dependance of the character of motion on the size of the tube and the velocity of the fluid, occurred to me until after the completion of my investigation on the transpiration of gases, in which was established the dependance of the law of transpiration on the relation between the size of the channel and the *mean range* of the gaseous molecules.

6. *Evidence of dimensional properties in the equations of motion.*—The equations of motion had been subjected to such close scrutiny, particularly by Professor STOKES, that there was small chance of discovering anything new or faulty in them. It seemed to me possible, however, that they might contain evidence which had been overlooked, of the dependance of the character of motion on a relation between the dimensional properties and the external circumstances of motion. Such evidence, not only of a connexion but of a definite connexion, was found, and this without integration.

If the motion be supposed to depend on a single velocity parameter U, say the mean velocity along a tube, and on a single linear parameter c, say the radius of the tube; then having in the usual manner eliminated the pressure from the equations, the accelerations are expressed in terms of two distinct types. In one of which

$$\frac{U^2}{c^2}$$

is a factor, and in the other

$$\frac{\mu U}{\rho c^2}$$

is a factor. So that the relative values of these terms vary respectively as U and

$$\frac{\mu}{c\rho}.$$

This is a definite relation of the exact kind for which I was in search. Of course without integration the equations only gave the relation without showing at all in what way the motion might depend upon it.

It seemed, however, to be certain if the eddies were owing to one particular cause, that integration would show the birth of eddies to depend on some definite value of

$$\frac{c\rho U}{\mu}$$

7. *The cause of eddies.*—There appeared to be two possible causes for the change of direct motion into sinuous. These are best discussed in the language of hydrodynamics, but as the results of this investigation relate to both these causes, which, although the distinction is subtle, are fundamentally distinct and lead to distinct results, it is necessary that they should be indicated.

The general cause of the change from steady to eddying motion was in 1843 pointed out by Professor STOKES as being that under certain circumstances the steady motion

becomes unstable, so that an indefinitely small disturbance may lead to a change to sinuous motion. Both the causes above referred to are of this kind, and yet they are distinct, the distinction lying in the part taken in the instability by viscosity.

If we imagine a fluid free from viscosity and absolutely free to glide over solid surfaces, then comparing such a fluid with a viscous fluid in exactly the same motion—

(1.) The frictionless fluid might be instable and the viscous fluid stable. Under these circumstances the cause of eddies is the instability as a perfect fluid, the effect of viscosity being in the direction of stability.

(2.) The frictionless fluid might be stable and the viscous fluid unstable, under which circumstances the cause of instability would be the viscosity.

It was clear to me that the conclusions I had drawn from the equations of motion immediately related only to the first cause; nor could I then perceive any possible way in which instability could result from viscosity. All the same I felt a certain amount of uncertainty in assuming the first cause of instability to be general. This uncertainty was the result of various considerations, but particularly from my having observed that eddies apparently come on in very different ways, according to a very definite circumstance of motion, which may be illustrated.

When in a channel the water is all moving in the same direction, the velocity being greatest in the middle and diminishing to zero at the sides, as indicated by the curve in fig. 1, eddies showed themselves reluctantly and irregularly; whereas when the

Fig. 1.

Fig. 2.

water on one side of the channel was moving in the opposite direction to that on the other, as shown by the curve in fig. 2, eddies appeared in the middle regularly and readily.

8. *Methods of investigation.*—There appeared to be two ways of proceeding—the one theoretical, the other practical.

The theoretical method involved the integration of the equations for unsteady

motion in a way that had not been accomplished and which, considering the general intractability of the equations, was not promising.

The practical method was to test the relation between U, $\frac{\mu}{\rho}$, and c; this, owing to the simple and definite form of the law, seemed to offer, at all events in the first place, a far more promising field of research.

The law of motion in a straight smooth tube offered the simplest possible circumstances and the most crucial test.

The existing experimental knowledge of the resistance of water in tubes, although very extensive, was in one important respect incomplete. The previous experiments might be divided into two classes: (1) those made under circumstances in which the law of resistance was as the square of the velocity, and (2) those made under circumstances in which the resistance varied as the velocity. There had not apparently been any attempt made to determine the exact circumstances under which the change of law took place.

Again, although it had been definitely pointed out that eddies would explain resistance as the square of the velocity, it did not appear that any definite experimental evidence of the existence of eddies in parallel tubes had been obtained, and much less was there any evidence as to whether the birth of eddies was simultaneous with the change in the law of resistance.

These open points may be best expressed in the form of queries to which the answers anticipated were in the affirmative.

(1.) What was the exact relation between the diameters of the pipes and the velocities of the water at which the law of resistance changed?

Was it at a certain value of

$$cU\,?$$

(2.) Did this change depend on the temperature, i.e., the viscosity of water? Was it at a certain value of

$$\rho\frac{U}{\mu}\,?$$

(3.) Were there eddies in parallel tubes?

(4.) Did steady motion hold up to a critical value and then eddies come in?

(5.) Did the eddies come in at a certain value of

$$\frac{\rho cU}{\mu}\,?$$

(6.) Did the eddies first make their appearance as small and then increase gradually with the velocity, or did they come in suddenly?

The bearing of the last query may not be obvious; but, as will appear in the sequel, its importance was such that, in spite of satisfactory answers to all the other queries, a negative answer to this, in respect of one particular class of motions, led me to the reconsideration of the supposed cause of instability.

The queries, as they are put, suggest two methods of experimenting:—

(1.) Measuring the resistances and velocities of different diameters, and with different temperatures of water.

(2.) Visual observation as to the appearance of eddies during the flow of water along tubes or open channels.

Both these methods have been adopted, but, as the questions relating to eddies had been the least studied, the second method was the first adopted.

9. *Experiments by visual observation.*—The most important of these experiments related to water moving in one direction along glass tubes. Besides this, however, experiments on fluids flowing in opposite directions in the same tube were made, also a third class of experiments, which related to motion in a flat channel of indefinite breadth.

These last-mentioned experiments resulted from an incidental observation during some experiments made in 1876 as to the effect of oil to prevent wind waves. As the result of this observation had no small influence in directing the course of this investigation, it may be well to describe it first.

10. *Eddies caused by the wind beneath the oiled surface of water.*—A few drops of oil on the windward side of a pond during a stiff breeze, having spread over the pond and completely calmed the surface as regards waves, the sheet of oil, if it may be so called, was observed to drift before the wind, and it was then particularly noticed that while close to, and for a considerable distance from the windward edge, the surface presented the appearance of *plate glass;* further from the edge the surface presented that irregular wavering appearance which has already been likened to that of sheet glass, which appearance was at the time noted as showing the existence of eddies beneath the surface.

Subsequent observation confirmed this first view. At a sufficient distance from the windward edge of an oil-calmed surface there are always eddies beneath the surface even when the wind is light. But the distance from the edge increases rapidly as the force of the wind diminishes, so that at a limited distance (10 or 20 feet) the eddies will come and go with the wind.

Without oil I was unable to perceive any indication of eddies. At first I thought that the waves might prevent their appearance even if they were there, but by careful observation I convinced myself that they were not there. It is not necessary to discuss these results here, although, as will appear, they have a very important bearing on the cause of instability.

11. *Experiments by means of colour bands in glass tubes.*—These were undertaken early in 1880; the final experiments were made on three tubes, Nos. 1, 2, and 3. The diameters of these were nearly 1 inch, $\frac{1}{2}$ inch, and $\frac{1}{4}$ inch. They were all about 4 feet 6 inches long, and fitted with trumpet mouthpieces, so that water might enter without disturbance.

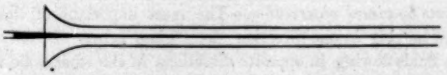
The water was drawn through the tubes out of a large glass tank, in which the

tubes were immersed, arrangements being made so that a streak or streaks of highly coloured water entered the tubes with the clear water.

The general results were as follows :—

(1.) When the velocities were sufficiently low, the streak of colour extended in a beautiful straight line through the tube, fig. 3.

Fig. 3.



(2.) If the water in the tank had not quite settled to rest, at sufficiently low velocities, the streak would shift about the tube, but there was no appearance of sinuosity.

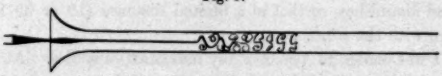
(3.) As the velocity was increased by small stages, at some point in the tube, always at a considerable distance from the trumpet or intake, the colour band would all at once mix up with the surrounding water, and fill the rest of the tube with a mass of coloured water, as in fig. 4.

Fig. 4.

Any increase in the velocity caused the point of break down to approach the trumpet, but with no velocities that were tried did it reach this.

On viewing the tube by the light of an electric spark, the mass of colour resolved itself into a mass of more or less distinct curls, showing eddies, as in fig. 5.

Fig. 5.



The experiments thus seemed to settle questions 3 and 4 in the affirmative, the existence of eddies and a critical velocity.

They also settled in the negative question 6, as to the eddies coming in gradually after the critical velocity was reached.

In order to obtain an answer to question 5, as to the law of the critical velocity, the diameters of the tubes were carefully measured, also the temperature of the water, and the rate of discharge.

(4.) It was then found that, with water at a constant temperature, and the tank as still as could by any means be brought about, the critical velocities at which the

eddies showed themselves were almost exactly in the inverse ratio of the diameters of the tubes.

(5.) That in all the tubes the critical velocity diminished as the temperature increased, the range being from 5° C. to 22° C.; and the law of this diminution, so far as could be determined, was in accordance with POISEUILLE's experiments. Taking T to express degrees centigrade, then by POISEUILLE's experiments,

$$\frac{\mu}{\rho} \propto P = (1 + 0{\cdot}0336\,T + 0{\cdot}00221\,T^2)^{-1}$$

taking a metre as the unit, U, the critical velocity, and D the diameter of the tube, the law of the critical point is completely expressed by the formula

$$U_c = \frac{1}{B_c}\,\frac{P}{D}$$

where

$$B_c = 43{\cdot}79$$
$$\log B_c = 1{\cdot}64139$$

This is a complete answer to question 5.

During the experiments many things were noticed which cannot be mentioned here, but two circumstances should be mentioned as emphasizing the negative answer to question 6. In the first place, the critical velocity was much higher than had been expected in pipes of such magnitude, resistance varying as the square of the velocity had been found at very much smaller velocities than those at which the eddies appeared when the water in the tank was steady; and in the second place, it was observed that the critical velocity was very sensitive to disturbance in the water before entering the tubes; and it was only by the greatest care as to the uniformity of the temperature of the tank and the stillness of the water that consistent results were obtained. This showed that the steady motion was unstable for large disturbances long before the critical velocity was reached, a fact which agreed with the full-blown manner in which the eddies appeared.

12. *Experiments with two streams in opposite directions in the same tube.*—A glass tube, 5 feet long and 1·2 inch in diameter, having its ends slightly bent up, as shown in fig. 6, was half filled with bisulphide of carbon, and then filled up with water and both

Fig. 6.

ends corked. The bisulphide was chosen as being a limpid liquid but little heavier than water and completely insoluble, the surface between the two liquids being clearly distinguishable. When the tube was placed in a horizontal direction, the weight of

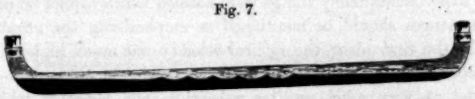
the bisulphide caused it to spread along the lower half of the tube, and the surface of separation of the two liquids extended along the axis of the tube. On one end of the tube being slightly raised the water would flow to the upper end and the bisulphide fall to the lower, causing opposite currents along the upper and lower halves of the tube, while in the middle of the tube the level of the surface of separation remained unaltered.

The particular purpose of this investigation was to ascertain whether there was a critical velocity at which waves or sinuosities would show themselves in the surface of separation.

It proved a very pretty experiment and completely answered its purpose.

When one end was raised quickly by a definite amount, the opposite velocities of the two liquids, which were greatest in the middle of the tube, attained a certain maximum value, depending on the inclination given to the tube. When this was small no signs of eddies or sinuosities showed themselves; but, at a certain definite inclination, waves (nearly stationary) showed themselves, presenting all the appearance of wind waves. These waves first made their appearance as very small waves of equal lengths, the length being comparable to the diameter of the tube.

Fig. 7.



When by increasing the rise the velocities of flow were increased, the waves kept the same length but became higher, and when the rise was sufficient the waves would curl and break, the one fluid winding itself into the other in regular eddies.

Whatever might be the cause, a skin formed slowly between the bisulphide and the water, and this skin produced similiar effects to that of oil on water; the results mentioned are those which were obtained before the skin showed itself. When the skin first came on regular waves ceased to form, and in their place the surface was disturbed, as if by irregular eddies, above and below, just as in the case of the oiled surface of water.

The experiment was not adapted to afford a definite measure of the velocities at which the various phenomena occurred; but it was obvious that the critical velocity at which the waves first appeared was many times smaller than the critical velocity in a tube of the same size when the motion was in one direction only. It was also clear that the critical velocity was nearly, if not quite, independent of any existing disturbance in the liquids; so that this experiment shows—

(1.) That there is a critical velocity in the case of opposite flow at which direct motion becomes unstable.

(2.) That the instability came on gradually and did not depend on the magnitude of the disturbances, or in other words, that for this class of motion question 6 must be answered in the affirmative.

It thus appeared that there was some difference in the cause of instability in the two motions.

13. *Further study of the equations of motion.*—Having now definite data to guide me, I was anxious to obtain a fuller explanation of these results from the equations of motion. I still saw only one way open to account for the instability, namely, by assuming the instability of a frictionless fluid to be general.

Having found a method of integrating the equations for frictionless fluid as far as to show whether any particular form of steady motion is stable for a small disturbance, I applied this method to the case of parallel flow in a *frictionless* fluid. The result, which I obtained at once, was that flow in one direction was stable, flow in opposite directions unstable. This was not what I was looking for, and I spent much time in trying to find a way out of it, but whatever objections my method of integration may be open to, I could make nothing less of it.

It was not until the end of 1882 that I abandoned further attempts with a frictionless fluid, and attempted by the same method the integration of a viscous fluid. This change was in consequence of a discovery that in previously considering the effect of viscoscity I had omitted to take fully into account the boundary conditions which resulted from the friction between the fluid and the solid boundary.

On taking these boundary conditions into account, it appeared that although the tendency of viscoscity through the fluid is to render direct or steady motion stable, yet owing to the boundary condition resulting from the friction at the solid surface, the motion of the fluid, irrespective of viscoscity, would be unstable. Of course this cannot be rendered intelligible without going into the mathematics. But what I want to point out is that this instability, as shown by the integration of the equations of motion, depends on exactly the same relation

$$U \propto \frac{\mu}{\rho}$$

as that previously found.

This explained all the practical anomalies and particularly the absence of eddies below a pure surface of water exposed to the wind. For in this case the surface being free, the boundary condition was absent, whereas the film of oil, by its tangential stiffness, introduced this condition; this circumstance alone seemed a sufficient verification of the theoretical conclusion.

But there was also the sudden way in which eddies came into existence in the experiments with the colour band, and the effect of disturbances to lower the critical velocity. These were also explained, for as long as the motion was steady, the instability depended upon the boundary action alone, but once eddies were introduced, the stability would be broken down.

It thus appeared that the meaning of the experimental results had been ascertained, and the relation between the four leading features and the circumstances on which they depend traced for the case of water in parallel flow.

But as it appeared that the critical velocity in the case of motion in one direction did not depend on the cause of instability with a view to which it was investigated, it followed that there must be another critical velocity, which would be the velocity at which previously existing eddies would die out, and the motion become steady as the water proceeded along the tube. This conclusion has been verified.

14. *Results of experiments on the law of resistance in tubes.*—The existence of the critical velocity described in the previous article could only be tested by allowing water in a high state of disturbance to enter a tube, and after flowing a sufficient distance for the eddies to die out, if they were going to die out, to test the motion.

As it seemed impossible to apply the method of colour bands, the test applied was that of the law of resistance as indicated in questions (1) and (2) in § 8. The result was very happy.

Two straight lead pipes No. 4 and No. 5, each 16 feet long and having diameters of a quarter and a half inch respectively were used. The water was allowed to flow through rather more than 10 feet before coming to the first gauge hole, the second gauge hole being 5 feet further along the pipe.

The results were very definite, and are partly shown in fig. 8, and more fully in diagram 1, Plate 74.

Fig. 8.

(1.) At the lower velocities the pressure was proportional to the velocity, and the velocities at which a deviation from the law first occurred were in exact inverse ratio of the diameters of the pipes.

(2.) Up to these critical velocities the discharge from the pipes agreed exactly with those given by POISEUILLE's formula for capillary tubes.

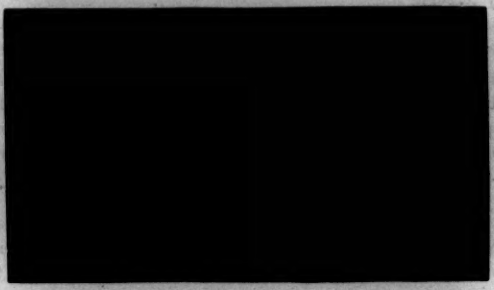
(3.) For some little distance after passing the critical velocity, no very simple relations appeared to hold between the pressures and velocities. But by the time the velocity reached 1·2 (critical velocity) the relation became again simple. The pressure did not vary as the square of the velocity, but as 1·722 power of the velocity, this law held in both tubes and through velocities ranging from 1 to 20, where it showed no signs of breaking down.

(4.) The most striking result was that not only at the critical velocity, but throughout the entire motion, the laws of resistance exactly corresponded for velocities in the ratio of

$$\frac{\mu}{\rho c}$$

This last result was brought out in the most striking manner on reducing the results by the graphic method of logarithmic homologues as described in my paper on Thermal Transpiration. Calling the resistance per unit of length as measured in the weight of cubic units of water i, and the velocity v, $\log i$ is taken for abscissa, and $\log v$ for ordinate, and the curve plotted.

In this way the experimental results for each tube are represented as a curve; these curves, which are shown as far as the small scale will admit in fig. 9, present exactly the same shape, and only differ in position.



Pipe.	Diameter. m.
No. 4, Lead	0·00615
„ 5, „	0·0127
A, Glass	0·0496
B, Cast iron	0·188
D, „	0·5
C, Varnish	0·196

Either of the curves may be brought into exact coincidence with the other by a rectangular shift, and the horizontal shifts are given by the difference of the logarithm of

$$\frac{D^3}{\mu^2}$$

for the two tubes, the vertical shifts being the difference of the logarithms of

$$\frac{D}{\mu}$$

The temperatures at which the experiment had been made were nearly the same, but not quite, so that the effect of the variations of μ showed themselves.

15. *Comparison with* DARCY'S *experiments.*—The definiteness of these results, their agreement with POISEUILLE'S law, and the new form which they more than indicated for the law of resistance above the critical velocities, led me to compare them with

the well known experiments of DARCY on pipes ranging from 0·014 to 0·5 metre in diameter.

Taking no notice of the empirical laws by which DARCY had endeavoured to represent his results, I had the logarithmic homologues drawn from his published experiments. If my law was general then these logarithmic curves, together with mine, should all shift into coincidence, if each were shifted horizontally through

$$\frac{D^3}{P^3}$$

and vertically through

$$\frac{D}{P}$$

In calculating these shifts there were some doubtful points. DARCY's pipes were not uniform between the gauge points, the sections varying as much as 20 per cent., and the temperature was only casually given. These matters rendered a close agreement unlikely. It was rather a question of seeing if there was any systematic disagreement. When the curves came to be shifted the agreement was remarkable. In only one respect was there any systematic disagreement, and this only raised another point; it was only in the slopes of the higher portions of the curves. In both my tubes the slopes were as 1·722 to 1; in DARCY's they varied according to the nature of the material, from the lead pipes, which were the same as mine, to 1·92 to 1 with the cast iron.

This seems to show that the nature of the surface of the pipe has an effect on the law of resistance above the critical velocity.

16. *The critical velocities.*—All the experiments agreed in giving

$$v_c = \frac{1}{278}\frac{P}{D}$$

as the critical velocity, to which corresponds as the critical slope of pressure

$$i_c = \frac{1}{47700000}\frac{P^2}{D^2}$$

the units being metres and degrees centigrade. It will be observed that this value is much less than the critical velocity at which steady motion broke down; the ratio being 43·7 to 278.

17. *The general law of resistance.*—The logarithmic homologues all consist of two straight branches, the lower branch inclined at 45 degrees and the upper one at n horizontal to 1 vertical. Except for the small distance beyond the critical velocity these branches constitute the curves. These two branches meet in a point on the curve at a definite distance below the critical pressure, so that, ignoring the small portion of the curve above the point before it again coincides with the upper branch, the logarithmic homologue gives for the law of resistance for all pipes and all velocities

$$A\frac{D^3}{\theta^2}i=(B\frac{D}{\theta}v)^n$$

where n has the value unity as long as either number is below unity, and then takes the value of the slope n to 1 for the particular surface of the pipe.

If the units are metres and degrees centigrade

$$A=67,700,000$$
$$B=396$$
$$P=(1+0{\cdot}0336\ T+0{\cdot}000221\ T^2)^{-1}$$

This equation then, excluding the region immediately about the critical velocity, gives the law of resistance in POISEUILLE's tubes, those of the present investigation and DARCY's, the range of diameters being

from 0·000013 (POISEUILLE, 1845)
to 0·5 (DARCY, 1857)

and the range of velocities

from 0·0026
to 7· } metres per sec., 1883.

This algebraical formula shows that the experiments entirely accord with the theoretical conclusions.

The empirical constants are A, B, P, and n; the first three relate solely to the dimensional properties of the fluid summed up in the viscosity, and it seems probable that the last relates to the properties of the surface of the pipe.

Much of the success of the experiments is due to the care and skill of Mr. FOSTER, of Owens College, who has constructed the apparatus and assisted me in making the experiments.

SECTION II.

Experiments in glass tubes by means of colour bands.

18. In commencing these experiments it was impossible to form any very definite idea of the velocity at which eddies might make their appearance with a particular tube. The experiments of POISEUILLE showed that the law of resistance varying as the velocity broke down in a pipe of say 0·6 millim. diameter; and the experiments of DARCY showed this law did not hold in a half-inch pipe with a velocity of 6 inches per second.

These considerations, together with the comparative ease with which experiments on a small scale can be made, led me to commence with the smallest tube in which I

could hope to perceive what was going on with the naked eye, expecting confidently that eddies would make their appearance at an easily attained velocity.

19. *The first apparatus.*—This consisted of a tube about $\frac{1}{4}$ inch or 6 millims. in diameter. This was bent into the siphon form having one straight limb about 2 feet long and the other about 5 feet (Plate 72, fig. 10).

The end of the shorter limb was expanded to a bell mouth, while the longer end was provided with an indiarubber extension on which was a screw clip.

The bell-mouthed limb was held vertically in the middle of a beaker with the mouth several inches from the bottom as shown in figs. 10 and 10′.

A colour tube about 6 millims. in diameter also of siphon form was placed as shown in the figure, with the open end of the shorter limb just under the bell mouth, the longer limb communicating through a controlling clip with a reservoir of highly coloured water placed at a sufficient height. A supply-pipe was led into the beaker for the purpose of filling it; but not with the idea of maintaining it full, as it seemed probable that the inflowing water would create too much disturbance, experience having shown how important perfect internal rest is to successful experiments with coloured water.

20. *The first experiment.*—The vessels and the siphons having been filled and allowed to stand for some hours so as to allow all internal notion to cease, the colour clip was opened so as to allow the colour to emerge slowly below the bell (Plate 73, fig. 11).

Then the clip on the running pipe was opened very gradually. The water was drawn in at the bell mouth, and the coloured water entered, at first taking the form of a candle flame (Plate 73, fig. 12), which continually elongated until it became a very fine streak, contracting immediately on leaving the colour-tube and extending all along the tube from the bell mouth to the outlet (fig. 10). On further opening the regulating clip so as to increase the velocity of flow, the supply of colour remaining unaltered, the only effect was to diminish the thickness of the colour band. This was again increased by increasing the supply of colour, and so on until the velocity was the greatest that circumstances would allow—until the clip was fully open. Still the colour band was perfectly clear and definite throughout the tube. It was apparent that if there were to be eddies it must be at a higher velocity. To obtain this about 2 feet more were added to the longer leg of the siphon which brought it down to the floor.

On trying the experiment with this addition the colour band was still clear and undisturbed.

So that for want of power to obtain greater velocity this experiment failed to show eddies.

When the supply pipe which filled the beaker was kept running during the experiment, it kept the water in the beaker in a certain state of disturbance. The effect of this disturbance was to disturb the colour band in the tube, but it was extremely

difficult to say whether this was due to the wavering of the colour band or to genuine eddies.

21. *The final apparatus.*—This was on a much larger scale than the first. A straight tube, nearly 5 feet long and about an inch in diameter, was selected from a large number as being the most nearly uniform, the variation of the diameter being less than 1-32nd of an inch.

The ends of this tube were ground off plane, and on the end which appeared slightly the larger was fitted a trumpet mouth of varnished wood, great care being taken to make the surface of the wood continuous with that of the glass (Plate 73, fig. 13).

The other end of the glass pipe was connected by means of an indiarubber washer with an iron pipe nearly 2 inches in diameter.

The iron pipe passed horizontally through the end of a tank, 6 feet long, 18 inches broad and 18 inches deep, and then bent through a quadrant so that it became vertical, and reached 7 feet below the glass tube. It then terminated in a large cock, having, when open, a clear way of nearly a square inch.

This cock was controlled by a long lever (see Plate 73) reaching up to the level of the tank. The tank was raised upon tressels about 7 feet above the floor, and on each side of it, at 4 feet from the ground, was a platform for the observers. The glass tube thus extended in an horizontal direction along the middle of the tank, and the trumpet mouth was something less than a foot from the end. Through this end, just opposite the trumpet, was a straight colour tube three-quarters of an inch in diameter, and this tube was connected, by means of an indiarubber tube with a clip upon it, with a reservoir of colour, which for good reasons subsequently took the form of a common water bottle.

With a view to determining the velocity of flow, an instrument was fitted for showing the changes of level of the water in the tank to the 100th of an inch (Plate 72, fig. 14). Thermometers were hung at various levels in the tank.

22. *The final experiments.*—The first experiment with this apparatus was made on 22nd February, 1880.

By means of a hose the tank was filled from the water main, and having been allowed to stand for several hours, from 10 A.M. to 2 P.M., it was then found that the water had a temperature of 46° F. at the bottom of the tank, and 47° F. at the top. The experiment was then commenced in the same manner as in the first trials. The colour was allowed to flow very slowly, and the cock slightly opened. The colour band established itself much as before, and remained beautifully steady as the velocity was increased until, all at once, on a slight further opening of the valve, at a point about two feet from the iron pipe, the colour band appeared to expand and mix with the water so as to fill the remainder of the pipe with a coloured cloud, of what appeared at first sight to be of a uniform tint (fig. 4, p. 942).

Closer inspection, however, showed the nature of this cloud. By moving the eye

so as to follow the motion of the water, the expansion of the colour band resolved itself into a well-defined waving motion of the band, at first without other disturbance, but after two or three waves came a succession of well-defined and distinct eddies. These were sufficiently recognisable by following them with the eye, but more distinctly seen by a flash from a spark, when they appeared as in fig. 5, p. 942.

The first time these were seen the velocity of the water was such that the tank fell 1 inch in 1 minute, which gave a velocity of 0^m627, or 2 feet per second. On slightly closing the valve the eddies disappeared, and the straight colour band established itself.

Having thus proved the existence of eddies, and that they came into existence at a certain definite velocity, attention was directed to the relations between this critical velocity, the size of the tube, and the viscosity.

Two more tubes (2 and 3) were prepared similar in length and mounting to the first, but having diameters of about one-half and one-quarter inch respectively.

In the meantime an attempt was made to ascertain the effect of viscosity by using water at different temperatures. The temperature of the water from the main was about 45°, the temperature of the room about 54°; to obtain a still higher temperature, the tank was heated to 70° by a jet of steam. Then taking, as nearly as we could tell, similar disturbances, the experiments which are numbered 1 and 2 in Table I. were made.

To compare these for the viscosity, POISEUILLE's experiments were available, but to prevent any accidental peculiarity of the water being overlooked, experiments after the same manner as POISEUILLE's were made with the water in the tank. The results of these however agreed so exactly with those of POISEUILLE that the comparative effect of viscosity was taken from POISEUILLE's formula

$$P^{-1}=1+0{\cdot}03368\,T+0{\cdot}000221\,T^2$$

where $P \propto \mu$ with the temperature and T is temperature centigrade.

The relative values of P at 47° and 70° Fah. are as

1·3936 to 1

while the relative critical velocities at these temperatures were as

1·45 to 1

which agreement is very close considering the nature of the experiments.

But whatever might have been the cause of the previous anomalies, these were greatly augmented in the heated tank. After being heated the tank had been allowed to stand for an hour or two, in order to become steady. On opening the valve it was thought that the eddies presented a different appearance from those in the colder water, and the thought at once suggested itself that this was due to some source of initial disturbance. Several sources of such disturbance suggested

themselves—the temperature of the tank was 11° C. above that of the room, and the cooling arising from the top and sides of the tank must cause circulation in the tank. A few streaks of colour added to the water soon showed that such a circulation existed, although it was very slow. Another source of possible disturbance was the difference in the temperature at the top and bottom of the tank, this had been as much as 5°.

In order to get rid of these sources of disturbance it was necessary to have the tank at the same temperature as the room, about 54° or 55°. Then it was found by several trials that the eddies came on at a fall of about 1 inch in 64 seconds, which, taking the viscosity into account, was higher than in the previous case, and this was taken to indicate that there was less disturbance in the water.

As it was difficult to alter the temperatures of the building so as to obtain experiments under like conditions at a higher temperature, and it appeared that the same object would be accomplished by cooling the water to its maximum density, 40°, this plan was adopted and answered well, ice being used to cool the water.

Experiments were then made with three tubes 1, 2, 3, at temperatures of about 51° and 40°. All are given in Table I.

TABLE I.

Experiments with Colour Bands—Critical Velocities at which Steady Motion breaks down.

Pipe No. 1, glass.—Diameter 0·0268 metre; log diameter $\bar{2}$·42828.
„ No. 2, „ „ 0·01527 „ „ $\bar{2}$·18400.
„ No. 3, „ „ 0·007886 „ „ $\bar{3}$·89783.
Discharge, cub. metre = ·021237; log = $\bar{2}$·32709.

Date, 1880.	Reference Number.	Pipe.	Temperature, centigrade.	Time of discharge.	Velocity, metres.	log time.	−log P.	log V.	log B_r.
1 March	1	No. 1.	8·3	60	0·6270	1·77815	0·11242	$\bar{1}$·79729	1·66200
3 „	2	„	21	87	0·4325	1·93959	0·25654	$\bar{1}$·63593	1·67930
25 „	3	„	15	70	0·5374	1·84500	0·19198	$\bar{1}$·73035	1·64936
21 April	4	„	12	60	0·6270	1·77815	0·15712	$\bar{1}$·79729	1·61730
„	5	„	13	64	0·5878	1·80618	0·16882	$\bar{1}$·76926	1·64464
„	6	„	13	67	0·5614	1·82617	0·16882	$\bar{1}$·74927	1·65368
„	7	„	13	64	0·5878	1·80618	0·16882	$\bar{1}$·76926	1·64464
„	8	„	5	54	0·6967	1·73239	0·06963	$\bar{1}$·84305	1·65898
„	9	„	5	52	0·7235	1·71600	0·06963	$\bar{1}$·85940	1·64269
22 „	10	„	10	62	0·6068	1·79239	0·13319	$\bar{1}$·78305	1·65546
„	11	„	11	64	0·5870	1·80613	0·14525	$\bar{1}$·76931	1·65716
25 March	12	No. 2.	22	155	0·7476	2·19033	0·26710	$\bar{1}$·87367	1·67523
23 April	13	„	11	110	1·052	2·04139	0·14525	0·02261	1·64814
„	14	„	11	108	1·072	2·03342	0·14525	0·03058	1·64017
„	15	„	4	83	1·396	1·91907	0·05621	0·14493	1·61486
„	16	„	4	83	1·396	1·91907	0·05621	0·14493	1·61486
„	17	„	4	83	1·396	1·91907	0·05621	0·14493	1·61486
„	18	„	6	86	1·348	1·93449	0·08278	0·12951	1·59371
„	19	„	6	85	1·362	1·92941	0·08278	0·13459	1·59863
24 „	20	No. 3.	11	220	1·967	2·34242	0·14525	0·29392	1·66300
„	21	„	10·5	224	1·932	2·35024	0·13920	0·28610	1·67687
„	22	„	11	218	1·982	2·33845	0·14525	0·29789	1·65903
„	23	„	11	116	2·004	2·33445	0·14525	0·30189	1·65503
25 „	24	„	4	164	2·637	2·21484	0·05621	0·42150	1·62446
„	25	„	4	172	2·517	2·23552	0·05621	0·40082	1·64514
„	26	„	6	176	2·460	2·24551	0·08278	0·39083	1·62856
„	27	„	6	176	2·460	2·24551	0·08278	0·39083	1·62856
„	28	„	6	174	2·488	2·24054	0·08278	0·39580	1·62359
„	29	„	6	177	2·446	2·24791	0·08278	0·38837	1·63102

This gives the mean value for log B, 1·64139; and B, = 43·79.

In reducing the results the unit taken has been the metre and the temperature is given in degrees centigrade.

The diameters of the three tubes were found by filling them with water.

The time measured was the time in which the tank fell 1 inch, which in cubic metres is given by

$$Q = \cdot 021237$$

In the table the logarithms of P, v, and B, are given, as well as the natural numbers for the sake of reference.

The velocities v have been obtained by the formula

$$v = \frac{4\,Q}{\pi\,D^2}$$

B, being obtained from the formula

$$B, = \frac{P}{vD}$$

The final value of B, is obtained from the mean value of the logarithm of B,.

23. *The results.*—The values of log B, show a considerable amount of regularity, and prove, I think conclusively, not only the existence of a critical velocity at which eddies come in, but that it is proportional to the viscosity and inversely proportional to the diameter of the tube.

The fact, however, that this relation has only been obtained by the utmost care to reduce the internal disturbances in the water to a minimum must not be lost sight of.

The fact that the steady motion breaks down suddenly shows that the fluid is in a state of instability for disturbances of the magnitude which cause it to break down. But the fact that in some conditions it will break down for a large disturbance, while it is stable for a smaller disturbance shows that there is a certain residual stability so long as the disturbances do not exceed a given amount.

The only idea that I had formed before commencing the experiments was that at some critical velocity the motion must become unstable, so that any disturbance from perfectly steady motion would result in eddies.

I had not been able to form any idea as to any particular form of disturbance being necessary. But experience having shown the impossibility of obtaining absolutely steady motion, I had not doubted but that appearance of eddies would be almost simultaneous with the condition of instability. I had not, therefore, considered the disturbances except to try and diminish them as much as possible. I had expected to see the eddies make their appearance as the velocity increased, at first in a slow or feeble manner, indicating that the water was but slightly unstable. And it was a matter of surprise to me to see the sudden force with which the eddies sprang into existence, showing a highly unstable condition to have existed at the time the steady motion broke down.

This at once suggested the idea that the condition might be one of instability for disturbance of a certain magnitude and stable for smaller disturbances.

In order to test this, an open coil of wire was placed in the tube so as to create a definite disturbance as in Plate 72, fig. 15.

Eddies now showed themselves at a velocity of less than half the previous critical velocity, and these eddies broke up the colour band, but it was difficult to say whether the motion was really unstable or whether the eddies were the result of the initial disturbance, for the colour band having once broken up and become mixed with the water, it was impossible to say whether the motion did not tend to become steady again later on in the tube.

Subsequent observation however tended to show that the critical value of the velocity depended to some extent on the initial steadiness of the water. One phenomenon in particular was very marked.

Where there was any considerable disturbance in the water of the tank and the cock was opened very gradually, the state of disturbance would first show itself by the wavering about of the colour band in the tube; sometimes it would be driven against the glass and would spread out, and all without a symptom of eddies. Then, as the velocity increased but was still comparatively small, eddies, and often very regular eddies, would show themselves along the latter part of the tube. On further opening the cock these eddies would disappear and the colour band would become fixed and steady right through the tube, which condition it would maintain until the velocity reached its normal critical value, and then the eddies would appear suddenly as before.

Another phenomenon very marked in the smaller tubes, was the intermittent character of the disturbance. The disturbance would suddenly come on through a certain length of the tube and pass away and then come on again, giving the appearance of flashes, and these flashes would often commence successively at one point in the pipe. The appearance when the flashes succeeded each other rapidly was as shown in Plate 72, fig. 16.

This condition of flashing was quite as marked when the water in the tank was very steady as when somewhat disturbed.

Under no circumstances would the disturbance occur nearer to the trumpet than about 30 diameters in any of the pipes, and the flashes generally, but not always, commenced at about this distance.

In the smaller tubes generally, and with the larger tube in the case of the ice-cold water at 40°, the first evidence of instability was an occasional flash beginning at the usual place and passing out as a disturbed patch two or three inches long. As the velocity was further increased these flashes became more frequent until the disturbance became general.

I did not see a way to any very crucial test as to whether the steady motion became unstable for a large disturbance before it did so for a small one; but the general impression left on my mind was that it did in some way—as though disturbances in

the tank, or arising from irregularities in the tube, were necessary to the existence of a state of instability.

But whatever these peculiarities may mean as to the way in which eddies present themselves, the broad fact of there being a critical value for the velocity at which the steady motion becomes unstable, which critical value is proportional to

$$\frac{\mu}{\rho c}$$

where c is the diameter of the pipe and $\frac{\mu}{\rho}$ the viscosity by the density, is abundantly established. And cylindrical glass pipes for approximately steady water have for the critical value

$$v = \frac{P}{B, D}$$

where in metres $B_1 = 43{\cdot}79$ about.

Section III.

Experiments to determine the critical velocity by means of resistance in the pipes.

24. Although at first sight such experiments may appear to be simple enough, yet when one began to consider actual ways and means, so many uncertainties and difficulties presented themselves that the necessary courage for undertaking them was only acquired after two years' further study of the hydrodynamical aspect of the subject by the light thrown upon it by the previous experiment with the colour bands. This has been already explained in Art. 13. Those experiments had shown definitely that there was a critical value of the velocity at which eddies began if the water were approximately steady when drawn into the tube, but they had also shown definitely that at such critical velocity the water in the tube was in a highly unstable condition, any considerable disturbance in the water causing the break down to occur at velocities much below the highest that could be attained when the water was at its steadiest; suggesting that if there were a critical velocity at which, for any disturbance whatever, the water became stable, this velocity was much less than that at which it would become unstable for infinitely small disturbances; or, in other words, suggesting that there were two critical values for the velocity in the tube, the one at which steady motion changed into eddies, the other at which eddies changed into steady motion.

Although the law for the critical value of the velocity had been suggested by the equations of motion, it was, as already explained, only at the beginning of this year that I succeeded in dealing with these equations so as to obtain any theoretical explanation of the dual criteria; but having at last found this, it became clear to me that if in a tube of sufficient length the water were at first admitted in a high state of disturbance, then as the water proceeded along the tube the disturbance would settle down into a steady condition, which condition would be one of eddies or steady

motion, according to whether the velocity was above or below what may be called the real critical value.

The necessity of initial disturbance precluded the method of colour bands, so that the only method left was to measure the resistance at the latter portion of the tube in conjunction with the discharge.

The necessary condition was somewhat difficult to obtain. The change in the law of resistance could only be ascertained by a series of experiments which had to be carried out under similar conditions as regards temperature, kind of water, and condition of the pipe; and in order that the experiments might be satisfactory, it seemed necessary that the range of velocities should extend far on each side of the critical velocity. In order to best ensure these conditions, it was resolved to draw the water direct from the Manchester main, using the pressure in the main for forcing the water through the pipes. The experiments were conducted in the workshop in Owens College, which offered considerable facilities owing to arrangements for supplying and measuring the water used in experimental turbines.

25. *The apparatus.*—This is shown in Plate 72, fig. 17.

As the critical value under consideration would be considerably below that found for the change for steady motion into eddies, a diameter of about half an inch (12 millims.) was chosen for the larger pipe, and one quarter of an inch for the smaller, such pipes being the smallest used in the previous experiments.

The pipes (4 and 5) were ordinary lead gas or water pipes. These, which owing to their construction are very uniform in diameter and when new present a bright metal surface inside, seemed well adapted for the purpose.

Pipes 4 (which was a quarter-inch pipe) and 5 (which was a half-inch) were 16 feet long, straightened by laying them in a trough formed by two inch boards at right angles. This trough was then fixed so that one side of the trough was vertical and the other horizontal, forming a horizontal ledge on which the pipes could rest at a distance of 7 feet from the floor; on the outflow ends of the pipes cocks were fitted to control the discharge, and at the inlet end the pipes were connected, by means of a T branch, with an indiarubber hose from the main; this connexion was purposely made in such a manner as to necessitate considerable disturbance in the water entering the pipes from the hose. The hose was connected, by means of a quarter-inch cock, with a four-inch branch from the main. With this arrangement the pressure on the inlet to the pipes was under control of the cock from the main, and at the same time the discharge from the pipes was under control from the cocks on their ends.

This double control was necessary owing to the varying pressure in the main, and after a few preliminary experiments a third and more delicate control, together with a pressure gauge, were added, so as to enable the observer to keep the pressure in the hose, *i.e.*, on the inlets to the pipes, constant during the experiments.

This arrangement was accomplished by two short branches between the hose and

the control cock from the main, one of these being furnished with an indiarubber mouthpiece with a screw clip upon it, so that part of the water which passed the cock might be allowed to run to waste, the other branch being connected with the lower end of a vertical glass tube, about 6 millims. in diameter and 30 inches long, having a bulb about 2 inches diameter near its lower extremity, and being closed by a similar bulb at its top.

This arrangement served as a delicate pressure gauge. The water entering at the lower end forced the air from the lower bulb into the upper, causing a pressure of about 30 inches of mercury. Any further rise increased this pressure by forcing the air in the tubes into the upper bulb, and by the weight of water in the tube. During an experiment the screw clip was continually adjusted, so as to keep the level of the water in the glass tube between the bulbs constant.

26. *The resistance gauges.*—Only the last 5 feet of the tube was used for measuring the resistance, the first 10 or 11 feet being allowed for the acquirement of a regular condition of flow.

It was a matter of guessing that 10 feet would be sufficient for this, but since, compared with the diameter, this length was double as great for the smaller tube, it was expected that any insufficiency would show itself in a greater irregularity of the results obtained with the larger tube, and as no such irregularity was noticed it appears to have been sufficient.

At distances of 5 feet near the ends of the pipe, two holes of about 1 millim. were pierced into each of the pipes for the purpose of gauging the pressures at these points of the pipes. As owing to the rapid motion of the water in the pipes past these holes, any burr or roughness caused in the inside of the pipe in piercing these holes would be apt to cause a disturbance in the pressure, it was very important that this should be avoided. This at first seemed difficult, as owing to the distance—5 feet—of one of the holes from the end of pipes of such small diameter the removal of a burr, which would be certain to ensue on drilling the holes from the outside, was difficult. This was overcome by the simple expedient suggested by Mr. Foster of drilling holes completely through the pipes and then plugging the side on which the drill entered. Trials were made, and it was found that the burr thus caused was very slight.

Before drilling the holes short tubes had been soldered to the pipes, so that the holes communicated with these tubes; these tubes were then connected with the limbs of a siphon gauge by indiarubber pipes.

These gauges were about 30 inches long; two were used, the one containing mercury, the other bisulphide of carbon.

These gauges were constructed by bending a piece of glass tube into a U form, so that the two limbs were parallel and at about one inch apart.

Glass tubes are seldom quite uniform in diameter, and there was a difference in the size of the limbs of both gauges, the difference being considerable in the case of the bisulphide of carbon.

The tubes were fixed to stands with carefully graduated scales behind them, so that the height of the mercury or carbon in each limb could be read. It had been anticipated that readings taken in this way would be sufficient. But it turned out to be desirable to read variations of level of the smallness of $\frac{1}{10000}$th of an inch or $\frac{1}{40}$th of a millimetre.

A species of cathetometer was used. This had been constructed for my experiments on Thermal Transpiration, and would read the position of the division surface of two fluids to $\frac{1}{10000}$th inch (Phil. Trans. 1879, p. 789).

The water was carefully brought into direct connexion with the fluid in the gauge, the indiarubber connexions facilitating the removal of all air.

27. *Means adopted in measuring the discharge.*—For many reasons it was very desirable to measure the rate of discharge in as short a time as possible.

For this purpose a species of orifice or weir gauge was constructed, consisting of a vertical tin cylinder two feet deep, having a flat bottom, being open at the top, with a diaphragm consisting of many thicknesses of fine wire gauze about two inches from the bottom; a tube connected the bottom with a vertical glass tube, the height of water in which showed the pressure of water on the bottom of the gauze; behind this tube was a scale divided so that the divisions were as the square roots of the height. Through the thin tin bottom were drilled six holes, one an eighth of an inch diameter, one a quarter of an inch, and four of half an inch.

These holes were closed by corks so that any one or any combination could be used. The combinations used were:

Gauge No. 1. The $\frac{1}{8}$ inch hole alone.
No. 2. The $\frac{1}{4}$ inch hole alone.
No. 3. A $\frac{1}{2}$ inch hole alone.
No. 4. Two $\frac{1}{4}$ inch holes.
No. 5. Four $\frac{1}{4}$ inch holes.

According to experience, the velocity with which water flows from a still vessel through a round hole in a thin horizontal plate is very nearly proportional to the area of the hole and the square root of the pressure, so that with any particular hole the relative quantities of water discharged would be read off at the variable height gauge. The accuracy of the gauge, as well as the absolute values of the readings, was checked by comparing the readings on the gauge with the time taken to fill vessels of known capacity. In this way coefficients for each one of the combinations 1, 2, 3, 4, 5 were obtained as follows:—

TABLE II.

No. of Gauge.	Readings on Gauge.	Time.	Quantity.	Coefficient.	Logarithmic coefficient.
		Seconds.	c.c.		
Gauge No. 1	19·55	61	1160	·966	1·985
ib.	—	59	1160		
No. 2	5·3	54	1160	4·055	·608
ib.	15·3 full	—	A	4·055	—
No. 3	15	360	A	16·220	1·210
No. 4	15	178	A	32·440	1·511
No. 5	15	90	A	64·880	1·812

From this table it will be seen that the absolute values of the coefficients were obtained from experiments on the gauges No. 1 and No. 2, the coefficients for the gauges 3, 4, and 5 being determined by comparison of the times taken to fill a vessel of unknown capacity, which stands in the Table as A. The relative value of these coefficients came out sensibly proportional to the squares of the diameters of the apertures.

For the smaller velocities it was found that the gauge No. 1 was too large, and in order not to delay the experiment in progress, two glass flasks were used: these are distinguished as flasks (1) and (2); their capacities, as subsequently determined with care, were 303 and 1160 c.c. The discharge as measured by the times taken to fill these flasks are reduced to c.c. per second by dividing the capacities of the flasks by the times.

28. *The method of carrying out the experiments.*—This was generally as follows:—My assistant, Mr. FOSTER, had charge of the supply of water from the main, keeping the water in the pressure gauge at a fixed level.

The tap at the end of the tube to be experimented upon being closed, the zero reading of the gauge was carefully marked, and the micrometer adjusted so that the spider line was on the division of water and fluid in the left hand limb of the gauge. The screw was then turned through one entire revolution, which lowered the spider line one-fiftieth of an inch; the tap at the end of the pipe was then adjusted until the fluid in the gauge came down to the spider line; having found that it was steady there, the discharge was measured.

This having been done, the spider line was lowered by another complete revolution of the screw, the tap again adjusted, and so on, for about 20 readings, which meant about half an inch difference in the gauge. Then the readings were taken for every five turns of the screw until the limit of the range, about 2 inches, was reached. After this, readings were taken by simple observation of the scale attached to the gauge. In taking these readings the best plan was to read the position of the mercury or carbon in both limbs of the gauge, but this was not always done, some of the

readings entered in the notes referred to one or other limb of the gauge, care having been taken to indicate which.

In the Tables III., IV., and V. of results appended, the noted readings are given and the letters r, l, and b signify whether the reading was on the right or left limb, or the sum of the readings on both limbs.

The readings marked l and r are reduced by the correction for the difference in the size of the limbs as well as the coefficient for the particular fluid in the gauge.

Thus it was found with the mercury tube that when the left limb had moved through 39 divisions on the scale the right had moved through 41, so that to obtain the sum of these readings the readings on the left, or those marked l, had to be multiplied by 2·05 and those on the right by 1·95.

With the bisulphide of carbon gauge, 11 divisions on the left caused 9 on the right, so that the correction for the reading on the left was 1·8 and on the right 2·2.

29. *Comparison of the pressure gauges.*—The pressures as marked by the gauges were reduced to the same standard by comparing the gauges; thus ·25 of the left limb of the mercury corresponded with 24 inches on both limbs of the bisulphide. Therefore to reduce the readings of the bisulphide of carbon to the same scale as those of the mercury they were multiplied by

$$\frac{\cdot 25 \times 20 \cdot 5}{24} = 0 \cdot 0213$$

This brought the readings of pressure to the same standard, *i.e.*, $\frac{1}{1000}$th of an inch of mercury, but these were further reduced by the factor 0·00032 to bring them to metres of water.

As it was convenient for the sake of comparison to obtain the differences of pressure per unit length of the pipe, the pressures in metres of water have been divided by 1·524, the length in metres between the gauge holes, and these reductions are included in the tables of results in the column headed i.

From the discharges as measured by the various gauges having been reduced to cubic centimetres, the mean velocity of the water was found by dividing by the area of the section of the pipe.

30. *Sections and diameters of the pipes.*—The areas were obtained by carefully measuring the diameters by means of fitting brass plugs into the pipes and then measuring the plugs. In this way the diameters were found to be—

Diameter, No. 4 pipe, ·242 inch, 6·15 millims.
„ No. 5 pipe, ·498 inch, 12·7 millims.

These gave the areas of the sections—

Section, No. 4 pipe, 29·7 square millims.
„ No. 5 pipe, 125 square millims.

The discharge in cubic centimetres divided by the area of section in square millimetres gave the mean velocity in metres per second as given in the Tables III., IV., and V.

The logarithms of i and v are given for the sake of comparison.

31. *The temperature.*—The chief reason why the water from the main had been used was from the necessity of having constant temperature throughout the experiments, and my previous experience of the great constancy of the temperature of the water in the mains, even over a period of some weeks.

At the commencement of the experiments the temperature of the water when flowing freely was found to be 5 C. or 41° F., and it remained the same throughout the experiments. Nevertheless, a fact which had been overlooked caused the temperature in the pipes to vary somewhat and in a manner somewhat difficult to determine.

This fact, which was not discovered until after the experiments had been reduced, was that the temperature of the workshop being above that of the main, the water would be warmed in flowing through the pipes to an extent depending on its flow. The possibility of this had not been altogether overlooked, and an early observation was made to see if any such warming occurred, but as it was found to be less than half a degree no further notice was taken until on reducing the results it was found that the velocities obtained with the very smallest discharges presented considerable discrepancies in various experiments; this suggested the cause.

The discrepancies were not serious if explained, so that all that was necessary was to carefully repeat the experiments at the lower velocities observing the temperatures of the effluent water. This was done, and further experiments were made (see Art. 33).

Table III.

Experiments on Resistance in Pipes made January 29, 1883.

Pipe No. 4, lead.—Diameter (as measured 0·242 inch), 6·15 millims. Length: total, 16 feet; to first gauge hole, 9·6 feet; between gauge holes (5 feet), 1·524 metres. Water from the Manchester Main.

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.				Velocity through orifice in thin plate.				Reduced to c.m. per second.	Centigrade.	Fahrenheit.				
				1. 303 c.c.	2. 1160 c.c.	3. 500 c.c.	4. 1000 c.c.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				i.	v.	$\log i$.	$\log v$.
1	20	..	0·0131	130	..	..	..	..	..	..	..	2·33	12	..	0·0086	0·0785	3·935	2·895
2	40	..	0·0262	69	..	..	..	..	..	..	..	4·40	..	..	0·01720	0·1480	2·236	1·170
3	60	..	0·0393	45	..	..	..	..	..	..	..	6·73	11	..	0·0258	0·2265	2·412	1·355
4	80	..	0·0524	34	..	..	..	..	..	..	..	8·91	..	..	0·0345	0·3000	2·537	1·477
5	100	..	0·0656	28	..	..	..	..	..	..	..	10·70	10	..	0·0430	0·3640	2·634	1·561
6	120	..	0·0787	23	..	..	..	..	..	..	..	13·2	9	..	0·0516	0·4426	2·713	1·646
7	140	Unsteady	0·0918	21	..	..	..	..	..	..	..	14·5	8	..	0·0602	0·4865	2·780	1·687
8	160	..	0·1040	..	80	..	..	..	..	..	..	14·5	7	..	0·0682	0·5106	2·834	1·708
9	160	..	0·1040	..	76	..	..	..	..	..	..	15·2	6	..	0·0682	0·5106	2·834	1·708
10	180	..	0·1181	..	71	..	..	..	..	..	..	16·3	..	..	0·0774	0·5483	2·889	1·739
11	200	..	0·1313	..	71	..	..	..	..	..	..	16·3	..	..	0·0861	0·5483	2·935	1·739
12	220	..	0·1443	..	69	..	..	..	..	..	..	16·8	..	..	0·0946	0·5650	2·976	1·752
13	240	..	0·1574	..	67	..	..	..	..	..	..	17·3	..	..	0·1033	0·5822	1·014	1·765
14	260	..	0·1707	..	66·5	..	..	..	..	..	..	17·4	..	..	0·1120	0·5862	1·049	1·768
15	280	..	0·1837	..	64	..	..	..	..	..	..	18·1	6	..	0·1206	0·6096	1·081	1·785
16	300	..	0·1968	..	61·5	..	..	..	..	..	..	18·8	..	..	0·1292	0·6339	1·111	1·802
17	320	..	0·2099	..	60	..	..	..	..	..	..	19·3	..	..	0·1378	0·6520	1·139	1·813

TABLE III. (continued).

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.				Velocity through orifice in thin plate.				Reduced to c.m. per second.	Centigrade.	Fahrenheit.			log i.	log v.
				1. 303 c.c.	2. 1160 c.c.	3. 500 c.c.	4. 1000 c.c.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				i.	v.		
18	320	..	0·2099	..	..	..	..	4·7	..	..	..	19·1	..	..	0·1378	0·6413	$\bar{1}$·139	$\bar{1}$·807
19	400	..	0·2613	..	54	..	..	5·3	..	..	..	21·5	..	..	0·1714	0·7228	$\bar{1}$·234	$\bar{1}$·859
20	500 *l*	..	0·3274	..	..	..	..	6·0	..	..	..	24·3	..	..	0·2148	0·8185	$\bar{1}$·332	$\bar{1}$·913
21	700	..	0·4592	..	..	..	..	7·4	..	..	..	30·0	..	..	0·3014	1·033	$\bar{1}$·479	0·014
22	1000	..	0·6562	..	..	..	..	9·4	..	..	..	38·1	..	..	0·4306	1·283	$\bar{1}$·634	0·108
23	1500	..	0·9355	..	..	..	..	11·7	..	..	..	47·5	5	..	0·6138	1·268	$\bar{1}$·788	0·103
24	2000	..	1·2480	..	..	..	..	13·6	..	..	..	55·1	..	..	0·8185	1·854	$\bar{1}$·913	0·268
25	2500	..	1·5560	..	..	..	..	15·8	..	..	..	64·2	..	..	1·021	2·158	0·009	0·334
26	3000	..	1·8710	..	..	..	..	17·5	..	..	..	71·0	..	..	1·228	2·388	0·089	0·378
27	3500	..	2·1830	..	..	..	..	19·1	..	..	..	79·1	..	..	1·433	2·661	0·156	0·425
28	4000 *r*	..	2·4950	..	..	..	..	20·1	..	..	..	81·1	..	..	1·637	2·729	0·214	0·436
29	4000	..	2·4950	..	..	..	..	..	4·9	..	..	79·5	..	..	1·637	2·674	0·214	0·427
30	5000	..	3·1120	..	..	..	..	..	5·7	..	..	92·5	..	..	2·042	3·112	0·310	0·493
31	6000	..	3·7420	..	..	..	..	..	6·5	..	..	105·0	..	..	2·455	3·540	0·390	0·549
32	7000	..	4·2660	..	..	..	..	..	7·1	..	..	115·0	..	..	2·865	3·873	0·457	0·588
33	8000	..	4·9890	..	..	..	..	..	7·7	..	..	125·0	..	..	3·274	4·198	0·515	0·623
34	8000 *l*	..	5·1290	..	..	..	..	..	8·0	..	..	130·0	..	..	3·444	4·467	0·537	0·650
35	9000	..	5·9030	..	..	..	..	..	8·6	..	..	139·0	5	..	3·873	4·689	0·588	0·671

Table IV.

Conditions the same as in Table III., except the temperatures at the lower velocities.

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.				Velocity through orifice in thin plate.				Reduced to c.m. per second.	Centigrade.	Fahrenheit.			log i.	log v.
				1. 303 c.c.	2. 1160 c.c.	3. 500 c.c.	4. 1000 c.c.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				i.	v.		
36	20	..	0·01313	..	..	227	..	..	..	..	..	1·750	10	50	0·008591	0·0740	3·934	2·869
37	40	..	0·02625	..	..	131	..	..	..	..	..	3·289	8	46·4	0·01718	0·1390	2·235	1·143
38	60	..	0·03936	..	..	80	..	..	..	..	..	4·966	7	44·6	0·02577	0·2100	2·411	1·322
39	80	..	0·05249	..	..	61	..	..	..	..	..	6·517	6	42·8	0·03436	0·2755	2·536	1·440
40	100	..	0·06562	..	..	50·5	..	..	..	..	..	7·871	5	41	0·04296	0·3327	2·633	1·522
41	120	..	0·07871	..	..	..	86	..	..	..	..	11·650	5	41	0·05153	0·3918	2·712	1·593
42	140	..	0·09184	..	..	..	76	..	..	..	..	13·16	5	41	0·06296	0·4426	2·779	1·646
43	160	..	0·1040	..	..	..	66	..	..	..	..	15·18	5	41	0·06808	0·5106	2·833	1·708
44	180	Unsteady	0·1181	..	..	..	62	..	..	..	..	16 15	5	41	0·07727	0·5433	2·888	1·735
45	200	..	0·1313	..	..	..	61	..	..	..	..	16·41	5	41	0·08591	0·5521	2·934	1·742
46	220	..	0·1443	..	..	..	60	..	..	..	..	16·52	5	41	0·09441	0·5560	2·975	1·745
47	240	..	0·1574	..	..	..	58	..	..	..	..	17·26	5	41	0·1031	0·5808	1·013	1·764
48	280	..	0·1837	..	..	..	55	..	..	..	..	18·20	5	41	0·1203	0·6124	1·080	1·787
49	320	..	0·2099	..	..	..	52	..	..	..	..	19·06	5	41	0·1375	0·6413	1·138	1·807
50	360	..	0·2250	..	..	..	50	..	..	..	..	20·00	5	41	0·1473	0·6730	1·168	1·828
51	400	..	0·2625	..	..	..	47	..	..	..	..	21·29	..	41	0·1718	0·7162	1·235	1·855

Table V.

Pipe No. 5, lead.—Diameter (as measured 0·498 inch), 12·7 millims. Length: total, 16 feet; to first gauge hole, 9·6 feet; between gauge holes (5 feet), 1·524 metres. Water from the Manchester Main.

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.			Velocity through orifice in thin plate.					Reduced to c.m. per second.	Centigrade.	Fahrenheit.			log *i*.	log *v*.
				1. 203 c.c.	2. 1160 c.c.	3. 500 c.c.	Gauge No. 1.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				*i*.	*v*.		
52	..	1	0·001219	..	..	..	4·5	..	..	..	..	4·346	12	..	0·00080	0·0346	4·902	2·539
53	..	2	0·002438	..	..	..	8·4	..	..	..	..	8·110	..	..	0·00159	0·0646	3·203	2·810
54	..	3	0·003656	..	..	..	11·2	..	..	..	..	9·841	..	..	0·00239	0·0784	3·379	2·894
55	..	4	0·004876	..	..	..	16·4	..	..	..	..	15·85	11	..	0·00319	0·1262	3·504	1·101
56	..	5	0·006082	..	..	..	..	4·4	..	..	..	17·83	..	..	0·00398	0·1420	3·600	1·152
57	..	6	0·007312	..	..	..	..	5·3	..	..	..	21·48	10	..	0·00478	0·1711	3·680	1·233
58	..	7 *l*	0·008532	..	..	..	..	6·0	..	..	..	24·33	..	..	0·00558	0·1937	3·747	1·287
59	..	8	0·009750	..	..	..	..	7·0	..	..	..	28·38	8	..	0·00638	0·2260	3·805	1·354
60	Unsteady	9	0·01097	..	..	..	..	7·0	..	..	..	28·38	..	..	0·00717	0·2260	3·856	1·354
61	..	10	0·01219	..	..	..	..	7·6	..	..	..	30·84	7	..	0·00798	0·2455	3·902	1·390
62	..	11	0·01340	..	..	..	..	8·0	..	..	..	32·44	..	..	0·00877	0·2583	3·943	1·412
63	..	20 *b*	0·01365	..	..	..	..	8·0	..	..	..	32·44	..	..	0·00893	0·2583	3·951	1·412
64	..	12	0·01463	..	..	..	..	8·4	..	..	..	34·05	..	..	0·00957	0·2710	3·981	1·433
65	..	13 *l*	0·01582	..	..	..	..	8·6	..	..	..	34·84	..	..	0·01036	0·2774	2·015	1·443
66	..	14	0·01707	..	..	..	..	8·8	..	..	..	35·65	..	..	0·01117	0·2838	2·048	1·453
67	..	15	0·01837	..	..	..	..	9·0	..	..	..	36·48	6	..	0·01203	0·2905	2·080	1·463

TABLE V. (continued).

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.			Velocity through orifice in thin plate.					Reduced to c.m. per second.	Centigrade.	Fahrenheit.				
				1. 303 c.c.	2. 1160 c.c.	3. 500 c.c.	Gauge No. 1.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				i.	v.	$\log i$.	$\log v$.
68	..	40	0·02729	..	..	..	..	10·8	..	..	..	43·76	..	..	0·01787	0·3484	2·252	1·542
69	..	60	0·04093	..	..	..	..	13·6	..	..	..	55·09	..	..	0·02680	0·4386	2·428	1·642
70	..	80	0·05458	..	..	..	..	16·3	..	..	..	66·07	..	..	0·03573	0·5261	2·553	1·721
71	..	100	0·06824	..	..	..	..	18·2	..	..	..	73·80	..	..	0·04467	0·5875	2·650	1·769
72	..	120	0·08185	..	..	..	..	20·2	..	..	..	81·85	..	..	0·05483	0·653	2·739	1·814
73	..	120	..	..	..	..	..	..	4·8	..	..	77·81	5	..	..	0·620	..	1·792
74	..	140	0·9550	..	..	..	..	..	5·2	..	..	84·34	..	..	0·06252	0·672	2·796	1·827
75	..	160	0·1092	..	..	..	..	..	5·8	..	..	93·98	..	..	0·07145	0·749	2·854	1·874
76	..	170	0·1159	..	..	..	..	..	6·0	..	..	97·28	..	..	0·07586	0·775	2·880	1·889
77	..	180	0·1228	..	..	..	..	..	6·3	..	..	102·1	..	..	0·08036	0·813	2·905	1·910
78	..	190	0·1295	..	..	..	..	..	6·5	..	..	105·2	..	..	0·08473	0·838	2·928	1·923
79	..	200	0·1365	..	..	..	..	..	6·6	..	..	107·0	..	..	0·08934	0·852	2·951	1·930
80	..	216	0·1433	..	..	..	..	..	6·8	..	..	110·2	..	..	0·09376	0·878	2·972	1·943
81	..	220	0·1500	..	..	..	..	..	7·0	..	..	113·6	..	..	0·09818	0·904	2·992	1·956
82	..	230	0·1567	..	..	..	..	..	7·3	..	..	118·4	..	..	0·1026	0·942	1·011	1·974
83	..	240	0·1637	..	..	..	..	..	7·5	..	..	121·7	..	..	0·1072	0·993	1·030	1·986
84	250	..	0·1637	..	..	..	..	..	7·5	..	..	..	5	..	0·1072	..	1·030	..
85	300	..	0·1968	..	..	..	..	..	8·6	..	..	139·4	..	..	0·1289	1·110	1·110	0·045

TABLE V. (continued).

Reference number.	Pressures.			Discharges.									Temperature.		Slope of pressure in water.	Velocity in metres per second.		
	Mercury in water.	Bisulphide of carbon in water.	Reduced to metres of water.	Time in seconds taken to fill flask.			Velocity through orifice in thin plate.					Reduced to c.m. per second.	Centigrade.	Fahrenheit.			log i.	log v.
				1. 303 c.c.	2. 1160 c.c.	3. 500 c.c.	Gauge No. 1.	Gauge No. 2.	Gauge No. 3.	Gauge No. 4.	Gauge No. 5.				i.	v.		
86	400	..	0·2625	..	..	..	..	..	10·3	..	..	166·8	..	..	0·1718	1·328	Ī·235	0·123
87	500	..	0·3281	..	..	..	..	..	11·7	..	..	189·7	..	..	0·2148	1·511	Ī·332	0·179
88	1,000	..	..	..	..	..	..	..	11·5	..	..	186·3	..	..	..	1·483	..	0·171
89	1,500	..	0·4798	..	..	..	..	..	14·2	..	..	230·2	..	..	0·3141	1·833	Ī·497	0·263
90	2,000	..	0·6398	..	..	..	..	..	17·3	..	..	280·6	..	..	0·4188	2·234	Ī·622	0·349
91	2,000	..	..	..	..	..	..	..	..	8·3	..	269·2	..	..	..	2·143	..	0·331
92	3,000	..	0·9595	..	..	..	..	..	..	10·8	..	350·0	..	..	0·6281	2·787	Ī·798	0·445
93	5,000	..	1·596	..	..	..	..	..	..	18·7	..	479·8	..	..	1·045	3·820	0·019	0·582
94	7,000	..	2·239	..	..	..	..	..	..	..	8·7	605·4	..	..	1·466	4·820	0·166	0·683
95	7,000	..	2·239	..	..	..	..	..	..	..	10·2	563·7	..	..	1·466	4·488	0·166	0·652
96	9,000	..	2·878	..	..	..	..	..	..	..	11·4	660·7	..	..	1·884	5·261	0·275	0·721
97	11,000	..	3·516	..	..	..	..	..	..	..	12·4	736·3	..	..	2·302	5·875	0·362	0·769
98	13,000	..	4·150	..	..	..	..	..	..	..	13·5	803·6	5	..	2·717	6·398	0·434	0·806
99	15,000	..	4·798	..	..	..	..	..	..	..	13·7	875·0	..	..	3·141	6·967	0·497	0·843
100	15,500	..	4·955	..	..	..	..	..	..	..	..	887·2	5	..	3·244	7·064	0·511	0·849

32. *The results of the experiments.*—A considerable number of preliminary experiments were made until the results showed a high degree of consistency. Then a complete series of experiments were made consecutively with each tube. The results of these are given in Tables III. and V.

33. *The critical velocities.*—The determination of these, which had been the main object of the experiments, was to some extent accomplished directly during the experiments, for starting from the very lowest velocities, it was found that the fluid in the differential gauge was at first very steady, lowering steadily as the velocity was increased by stages, until a certain point was reached, when there seemed to be something wrong with the gauge. The fluid jumped about, and the smallest adjustment of the tap controlling the velocity sent the fluid in the gauge out of the field of the microscope. At first this unsteadiness always came upon me as a matter of surprise, but after repeating the experiments several times, I learnt to know exactly when to expect it. The point at which this unsteadiness is noted is marked in the tables.

It was not, however, by the unsteadiness of the pressure gauge that the critical velocity was supposed to be determined, but by comparing the ratio of velocities and pressures given in the columns v and i in the tables. This comparison is shown in diagram I., Plate 74, the values of i being abscissæ and v ordinates. It is thus seen that for each tube the points which mark the experiments lie very nearly in a straight line up to definite points marked C, at which divergence sets in rapidly.

The points at which this divergence occurs correspond with the experiments numbered 6 and 59, which are immediately above those marked unsteady.

Thus the change in the law of pressure agrees with the observation of unsteadiness in fixing the critical velocities.

According to my assumption, the straightness of the curves between the origin and the critical points would depend on the constancy of temperature, and it was the small divergences observed that suggested a variation of temperature which had been overlooked. This variation was confirmed by further experiments, amongst which are those contained in Table IV. These showed that the probable variation of the temperature was in Table III. from 12° C. to 9° C. at the critical point, and from 12° C. to 8° C. in Table V., which variations would account for the small deviation from the straight.

It only remained, then, to ascertain how far the actual values of v_c, the velocity at the critical points, corresponded with the ratio $\frac{\mu}{D}$ or $\frac{P}{D}$.

For tube 4 from the Table III.

$$D = 0^{m}{\cdot}00615$$

$$v_c = 0^{m}{\cdot}4426$$

at 9° C.; at this temperature

$$P = {\cdot}757$$

see p. 952.

Hence putting

$$B_c = \frac{P}{v_c D}$$

we have

$$B_c = 279{\cdot}7$$

Again, for tube 5, Table V.

$$D = {\cdot}0127$$

$$v_c = {\cdot}2260$$

at 8° C.; at which temperature

$$P = {\cdot}7796$$

whence

$$B_c = 272{\cdot}0$$

The differences in the values of B_c thus obtained would be accounted for by a variation of a quarter of a degree in temperature, and hence the results are well within the accuracy of the experiments.

To each critical velocity, of course, there corresponds a critical value of the pressure. These are determined as follows.

The theoretical law of resistance for steady motion may be expressed

$$A_c D^3 i = B_c P v$$

and multiplying both sides by $\frac{D}{P^3}$

$$\frac{A_c D^4 i}{P^3} = B_c \frac{D}{P} v$$

This law holds up to the critical velocity, and then the right hand number is unity if B_c has the values just determined.

$$A_c = \frac{P^3}{D^3 i_c}$$

by Table III.

$$i_c = {\cdot}0516$$

$$P^3 = {\cdot}573$$

$$D^3 = {\cdot}000{,}000{,}232$$

which give

$$A_c = 47{,}750{,}000$$

By Table V.

$$i_c = {\cdot}00638$$

$$P^3 = {\cdot}607$$

$$D^3 = {\cdot}00000205$$

which give

$$A_c = 46{,}460{,}000$$

which values of A_c differ by less than by what would be caused by half a degree of temperature.

The conclusion, therefore, that the critical velocity would vary as

$$\frac{\mu}{D}$$

is abundantly verified.

34. *Comparison with the discharges calculated by* POISEUILLE'S *formula.*—POISEUILLE experimented on capillary tubes of glass between ·02 and ·1 millim. in diameter, and it is a matter of no small interest to find that the formula of discharges which he obtained from these experiments is numerically exact for the bright metal tubes 100 times as large.

POISEUILLE'S formula is—

$$Q=1836{\cdot}724(1+0{\cdot}0336793\,T+0{\cdot}000220992\,T^2)\frac{HD^4}{L}$$

T = temperature in degrees centigrade.
H = pressure in millims. mercury.
D = diameter in millims.
L = length in millims.
Q = discharge in millims. cubed.

Putting

$$i=\frac{13{\cdot}64H}{L}$$

$$P=1+(0{\cdot}336793\,T+0{\cdot}000220992\,T^2)^{-1}$$

$$v=\frac{4Q}{\pi D^3}$$

and changing the units to metres and cubic metres this formula may be written

$$47700000\frac{D^3}{P^2}i=278\frac{D}{P}v$$

the coefficients corresponding to A_r and B_r.

The agreement of this formula with the experimental results from tubes 4 and 5 is at once evident. The actual and calculated discharges differ by less than 2 per cent., a difference which would be more than accounted for by an error of half a degree in the temperature.

35. *Beyond the critical point.*—The tables show that, beyond the critical point, the relation between i and v differs greatly from that of a constant ratio; but what the exact relation is, and how far it corresponds in the two tubes, is not to be directly seen from the tables.

In the curves (Plate 74, diagram I.) which result from plotting i and v, it appears that after a period of flatness the curves round off into a parabolic form; but whether they are exact parabolæ, or how far the two curves are similar with different parameters, is difficult to ascertain by any actual comparison of the curves themselves, which, if plotted to a scale which will render the small differences of pressure visible, must extend 10 feet at least.

36. *The logarithmic method.*—So far the comparison of the results has been effected by the natural numbers, but a far more general and clearer comparison is effected by treating the logarithms of l and v.

This method of treating such experimental results was introduced in my paper on Thermal Transpiration (see Phil. Trans., Part II., 1879, p. 753).

Instead of curves, of which i and v are the abscissæ and ordinates, log i and log v are taken for the abscissæ and ordinates, and the curve so obtained is the logarithmic homologue of the natural curve.

The advantage of the logarithmic homologues is that the *shape* of the curve is made independent of any constant parameters, such parameters affecting the position of all points on the logarithmic homologue similarly. Any similarities in shape in the natural curves become identities in shape in the logarithmic homologues. How admirably adapted these logarithmic homologues are for the purpose in hand is at once seen from diagram II., Plate 73, which contains the logarithmic homologues of the curves for both pipes 4 and 5.

A glance shows the similarity of these curves, and also their general character. But it is by tracing one of the curves, and shifting the paper rectangularly until the traced curve is superimposed on the other, that the exact similarity is brought out. It appears that, without turning the paper at all, the two curves almost absolutely fit.

It also appears that the horizontal and vertical components of the shift are—

Horizontal shift	·913
Vertical shift	·294

which are within the accuracy of the work respectively identical with the differences of the logarithms of $\frac{D^3}{P^2}$ and $\frac{D}{P}$ for the two tubes.

37. *The general law of resistance in pipes.*—The agreement of the logarithmic homologues shows that not only at the critical velocities but for all velocities in these two pipes, pressure which renders $\frac{D^3}{\mu^2}i$ the same in both pipes corresponds to velocities which render $\frac{D}{\mu}v$ the same in both pipes. This may be expressed in several ways. Thus if the tabular value of i for each pipe plotted in a scale be multiplied by a number proportional to $\frac{D^3}{P^2}$ for that particular pipe and the values of v by a number proportional to $\frac{D}{P}$, then the curves which have these reduced values of i and v for abscissæ and ordinates will be identical.

A still more general expression is that if

$$i = F(v)$$

expresses the relation between i and v for a pipe in which $D = 1$, $T = 0$, $P = 1$.

$$\frac{D^3 i}{P^2} = F\left(\frac{Dv}{P}\right)$$

expresses the relation for every pipe and every condition of the water.

The determination of the relation between circumstances of motion and the physical condition of the water in such a general form was not contemplated when the experiments were undertaken, and must be considered as a result of the method of logarithmic homologues which brought out the relation in such a marked manner that it could not be overlooked. Nor is this all.

It had formed no part of my original intention to re-investigate the law of resistance in pipes for velocities above the critical value, as this is ground which had been very much experimented upon, and experiments seemed to show that the law was either indefinite or very complex—a conclusion which did not seem inconsistent with the supposition that above this point the resistance depended upon eddies which might be somewhat uncertain in their action. But although it was not my intention to investigate laws, I had made a point of continuing the experiments through a range of pressures and velocities very much greater I think than had ever been attempted in the same pipe.

Thus it will be noticed that in the larger tube the pressure in the last experiment is four thousand times as large as in the first. In choosing the great range of pressures I wished to bring out what previous experiments had led me to expect, namely, that in the same tube for sufficiently small pressures the pressure is proportional to the velocity, and for sufficiently great pressures, the pressure was proportional to the square of the velocity. Had this been the case not only would the lowest portion of the logarithmic homologues up to the critical point have come out straight lines inclined at 45 degrees, but the final portion of the curve would have come out a straight line at half this inclination, or with a slope of two horizontal to one vertical.

The near approach of the lower portions of the curve to the line at 45° led me, as I have already explained, to discover that the temperatures had risen at the lower velocities, and to make a fresh set of experiments, some of which are given in Table IV., in which, although the temperatures were not constant, they were sufficiently different from the previous ones to show that the discrepancy in the lower portions of the curves might be attributed to variations of temperature, and the agreement with the line of 45° considered as within the limits of accuracy of experiment.

When the logarithms of the upper portions of the curve came to be plotted, the straightness and parallelism of the two lines was very striking.

There are a few discrepancies which could not be in any way attributed to temperature, as with so much water moving this was very constant, but on examination it was seen that these discrepancies marked the changes of the discharge gauges. The law of flow through the orifices not having been strictly as the square roots of the heights, the manner in which the gauges had been compared forbade the possibility of there being a general error from this cause; the middle readings on the gauge were correct, so that the discrepancies, which are small, are mere local errors.

This left it clear that whatever might be their inclination the lines expressed the laws of pressures and velocities in both tubes, and since the lines are strictly parallel,

this law was independent of the diameter of the tube. This point has been very carefully examined, for it is found that the inclination of these lines differs decidedly from that of 2 to 1, being 1·723 to 1, and so giving a law of pressures through a range 1 to 50 of

$$i \propto v^{1\cdot723}$$

This is different from the law propounded by any of the previous experimenters, who have adhered to the laws

$$i = v^2$$

or

$$i = Av + Bv^2$$

That neither of these laws would answer in case of the present experiments was definitely shown, for the first of these would have a logarithmic homologue inclined at 2 to 1, and the second would have a curved line. A straight logarithmic homologue inclined at a slope 1·723 to 1 means no other law than

$$i \propto v^{1\cdot723}$$

I have therefore been at some pains to express the law deduced from my experiments on the uniform pipes so that it may be convenient for application. This law as already expressed is simply

$$\frac{D^s}{P^2} i = f\left(\frac{Dv}{P}\right)$$

where f is such that

$$x = f(y)$$

is the equation to the curve which would result from plotting the resistance and velocities in a pipe of diameter 1 at a temperature zero.

The exact form of f is complex, this complexity is however confined to the region immediately after the critical point is passed.

Up to the critical point

$$A_c \frac{D^s}{P^2} i = B_c \frac{Dv}{P}$$

After the critical point is passed the law is complex until a velocity which is 1·325 v_c is reached. Then as shown in the homologues the curve assumes a simple character again

$$A \frac{D^s}{P^2} i = \left(B \frac{Dv}{P}\right)^{1\cdot723}$$

that is, the logarithmic homologue becomes a straight line inclined at 1·723 to 1.

Referring to the logarithmic homologues (Plate 73, diagram II.), it will be seen that although the directions of the two straight extremities of the curve do not meet in the

critical point, their intersection is at a constant distance from this point which in the logarithmic curves is, both for ordinates and abscissæ,

$$0{\cdot}154$$

These points o are therefore given by

$$\log\frac{D^2i_o}{P^2}=\log\frac{D^2i_c}{P^2}+0{\cdot}154$$

$$\log\frac{Dv_o}{P}=\log\frac{Dv_c}{P}+0{\cdot}154$$

Therefore putting

$$A=\frac{P^2}{D^2i_c},\ B=\frac{P}{Dv_c}$$

$$\log A=\log A_c+0{\cdot}154$$

$$\log B=\log B_c+0{\cdot}154$$

and by the values of A_c and B_c previously ascertained (Art. 33, p. 971),

$$\log A=8{\cdot}8311 \qquad A=67{,}700{,}000$$

$$\log B=2{\cdot}598 \qquad B=\ 396{\cdot}3$$

We thus have for the equation to the curves corresponding to the upper straight branches

$$A\frac{D^2}{P^2}i=\left(B\frac{Dv}{P}\right)^{1{\cdot}723}$$

And if n have the value 1 or 1·722 according as either member of this equation is $<$ or $>$ 1 the equation

$$A\frac{D^2}{P^2}i=\left(\frac{BDv}{P}\right)^n$$

is the equation to a curve which has for its logarithmic homologue the two straight branches intersecting in o, and hence gives the law of pressures and velocities, except those relating to velocities in the neighbourhood of the critical point, and these are seldom come across in practice.

By expressing n as a discontinuous function of $B_c\frac{Dv}{P}$ the equation may be made to fit the curve throughout.

38. *The effect of temperature.*—It should be noticed that although the range is comparatively small, still the displacement of the critical point in Tables III. and IV. is distinctly marked. The temperatures were respectively 9° C., 5° C.

$$\text{At } 9°\ \log P^{-1}=0{\cdot}12093$$

$$\text{At } 5°\ \log P^{-1}=0{\cdot}06963$$

$$\text{Difference} \quad =\ 05130$$

This should be the differences in the values of log v, in Tables III. and IV. The actual difference is ·062. Also the differences in log i, should be the differences in P^2 or ·10260, whereas the actual difference is ·121.

The errors correspond to a difference of about 1° C., which is a very probable error.

It would be desirable to make experiments at higher temperature, but there were great difficulties about this which caused me, at all events for the time, to defer the attempt.

Section IV.

Application to Darcy's *experiments.*

39. Darcy's *experiments.*—The law of resistance came out so definitely from my experiments that, although beyond my original intention, I felt constrained to examine such evidence as could be obtained of the actual experimental results obtained by previous experimenters.

The lower velocities, up to the critical value, were found, as has already been shown (Art. 35), to agree exactly with Poiseuille's formula.

For velocities above the critical values the most important experiments were those of Darcy—approved by the Academy of Sciences and published 1845—on which the formula in general use has been founded. Notwithstanding that the formula as propounded by Darcy himself could not by any possibility fit the results which I have obtained, it seemed possible that the experiments on which he had based his law might fit my law. A comparison was therefore undertaken.

This was comparatively easy, as Darcy's experimental results have been published in detail.

Altogether he experimented on some 22 pipes, varying in diameter from about the size of my largest, 0^m·0014 up to 0^m·5. They were treated in several sets, according to the material of which they were composed—wrought iron gas pipes, lead pipes, varnished iron pipes, glass pipes, new cast iron and old rusty pipes.

The method of experimenting did not differ from mine except in scale, the distance between Darcy's gauge points being 50^m instead of 5 feet in my case. The great length between Darcy's gauge points entailed his having joints in his pipes between these points, and the nature of his pipes was such as to preclude the possibility of a very uniform diameter. His experiments appear to have been made with extreme care and very faithfully recorded, but the irregularity in the diameters, which appears to have been as much as 10 per cent., and the further irregularity of the joints, preclude the possibility of the results of his experiments following very closely the law for uniform pipes. Another important matter to which Darcy appears to have paid but little attention was temperature. It is true that in many instances he has given the temperature, but he does not appear to have taken any account of it in his discussion of his results, although it varied as much as 20° C. in the cases where he has given

it, and as his pipes, 300 metres long, were in the open air, the effect of the sun on the pipes would have led to still larger differences.

The effect of these various causes on his results may be seen, as he took the precaution to use two pressure gauges on separate lengths of 50m of his pipes, and the records from these two gauges by no means always agree, particularly for the lower velocities. In one case the results are as wide apart as 15 and 7, and often 10 or 15 per cent. In arriving at tabular values for i he has taken the mean of the two gauges.

Taking these things into account, I could not possibly expect any close agreement with my results; still, as experiments on pipes of such large diameters are not likely to be repeated, at any rate with anything like the same care and success, they offered the only chance of proving that my law was general.

40. *Reduction of the experimental results.*—Rejecting all the experiments on rusty and rough pipes, *i.e.*, selecting the lead, the varnished, the glass, and new cast iron pipes, which ranged from half-an-inch to twenty inches diameter, I had the logarithmic homologues drawn. These are shown on diagram III., Plate 74. In the case of two of the smaller pipes the smallest velocity is well below the critical point, and in several of the other pipes the smallest velocity is near the critical velocity. This accounts for the lower ends of the logarithmic curves being somewhat twisted; for the remainder of the logarithmic homologues are nearly straight; some are slightly bent one way and some another, but they are none of them more bent than may be attributed to experimental inaccuracy.

The inclinations of the upper ends of the lead and bituminous pipes is 1·746, slightly greater than mine; but in the cases of the glass pipes and the cast iron pipes the slopes are 1·82 and 1·92 respectively.

So much appeared from the logarithmic homologues themselves, but the most important question was, would the curves agree with the results calculated from the formula

$$A\frac{D^3}{P^2}i=\left(B\frac{D}{P}v\right)^n$$

41. *Comparison with the law of resistance.*—In applying this test I was at first somewhat at a loss on account in some cases of the want of any record of the temperature, and the doubt as to such temperatures as had been recorded being the temperature of the water in the pipes between the gauges.

The dates at which the experiments were made to a certain extent supplied the deficiency of temperature, the temperatures given fixing the law of temperature, so that the probable temperature could be assumed where it was not given.

Assuming the temperature, the values of

$$i_o=\frac{P^2}{AD^3}$$

$$v_o=\frac{P}{BD}$$

were calculated for each tube, using the values of A and B as already determined, $\log i$, and v_0 are the co-ordinates of O the intersection of the two straight branches of the logarithmic curves, so that the application of the formula to the results was simply tested by continuing the straight upper branches of the logarithmic homologues to see whether they passed through the corresponding point O.

The agreement, which is shown in diagram III., Plate 74, is remarkable. There are some discrepancies, but nothing which may not be explained by inaccuracies, particularly inaccuracies of temperature.

42. *The effect of the temperature above the critical point.*—It is a fact of striking significance, physical as well as practical, that while the temperature of the fluid has such an effect at the lower velocities that, *cæteris paribus*, the discharge will be double at 45° C. what it is at 5° C., so little is the effect at the higher velocities that neither DARCY or any other experimenter seems to have perceived any effect at all.

In my experiments the temperature was constant, 5° C. at the higher velocities, so that I had no cause to raise this point till I came to DARCY'S result, and then, after perplexing myself considerably to make out what the temperatures were, I noticed the effect of the temperature is to shift the curves 2 horizontal to 1 vertical, which corresponds with a slope of 2 to 1, and so nearly corresponds with the direction of the curves at higher velocities that variations of 5° or 10° C. produce no sensible effect; or, in other words, the law of resistance at the higher velocity is sensibly independent of the temperature, *i.e.*, of the viscosity.

Thus not only does the critical point, the velocity at which eddies come in, diminish with the viscosity, but the resistance after the eddies are established is nearly, if not quite, independent of the viscosity.

43. *The inclinations of the logarithmic curves.*—Although the general agreement of the logarithmic homologues completely establishes the relations between the diameters of the pipes, the pressures and velocities for each of the four classes of pipes tried, viz., the lead, the varnished pipes, the glass pipes, and the cast iron, there are certain differences in the laws connecting the pressures and velocity in the pipes of different material. In the logarithmic curves this is very clearly shown as a slight but definite difference between the inclination of the logarithmic homologues for the higher velocities.

The variety of the pipes tried reduces the possible causes of this difference to a small compass. It cannot be due to any difference in diameters, as at least three pipes of widely different diameters belong to each slope. It is not due to temperature. This reduces the cause for the different values of n to the irregularity in the pipes owing to joints and other causes, and the nature of the surfaces.

The effect of the joints on the values of n seems to be proved by the fact that DARCY'S three lead pipes gave slightly different values for n, while my two pipes without joints gave exactly the same value, which is slightly less than that obtained from DARCY'S experiments.

DARCY'S pipes were all of them uneven between the gauge points, the glass and the iron varying as much as 20 per cent. in section. The lead were by far the most uniform, so that it is not impossible that the differences in the values of n may be due to this unevenness.

But the number of joints and unevenness of the tarred pipes corresponded very nearly with the new cast iron, and between these there is a very decided difference in the value of n. This must be attributed to the roughness of the cast iron surface.

44. *Description of Diagram* III.

Diagram III.—In this diagram the experiments of POISEUILLE and DARCY are brought into comparison with those of the present investigation.

In consequence of the number of lines, the general aspect of the diagram is somewhat confused, but such confusion vanishes so soon as it is clearly perceived that each line of dots indicates the logarithmic homologue for some particular pipe as determined by experiment, reduced and plotted in exactly the same manner as for diagram II.; DD and EE being exact repetitions of the logarithmic homologue for pipes 4 and 5, on a somewhat smaller scale.

It is at once apparent from diagram III. how, for the most part, the experiments have been well below or well above the critical values. In the small pipes of POISEUILLE the velocities were below the critical values, and hence lie in straight lines inclined at 45°.

The smallest pipe on which POISEUILLE's experimented had a diameter of 0·014 millim.; only one experiment, marked A, is shown in the diagram, as the remaining three extended outside the range of the plate. They fall exactly on the dotted line through A, and do not reach the critical value.

The same is true of all the rest of POISEUILLE's experiments except those made on a much larger pipe, diameter 0·65 millim., hence it is thought sufficient to plot only one, namely BB.

CC shows the experimental results obtained with the pipe 0·65 millim. diameter, and these reach the critical value as given by the formula, and then diverge from the line.

It is important to notice, however, that the points are not taken directly from POISEUILLE's experiments, which have been subjected to a correction rendered necessary by the fact that POISEUILLE did not measure the resistance by ascertaining the pressure at two points in the pipe, but by ascertaining the pressure in the vessels from which and into which the water flowed through the pipe, so that his resistance includes, besides the resistance of the pipe, the pressure necessary to impart the initial velocity to the water. This fact, which appears to have been entirely overlooked, had a very important influence on many of POISEUILLE's results. POISEUILLE endeavoured to ascertain what was the limit to the application of his law, and, with the exception

of his smallest tubes, succeeded in attaining velocities at which the results were no longer in accordance with his law.

When I first examined his experiments I expected to find these limiting velocities above the critical velocities as given by my formula. In all cases, however, they were very much below, and it was then I came to see that POISEUILLE had taken no account of the pressure necessary to start the fluid.

It then became interesting to see how far the deviations were to be explained in this way.

In pipes of sensible size the pressure necessary to start the fluid lies between

$$\frac{v^2}{2g} \text{ and } 1{\cdot}505\,\frac{v^2}{2g}$$

according to whether the mouthpiece is trumpet-shaped or cylindrical. POISEUILLE states that he was careful to keep both ends of his pipe cylindrical, hence according to the law for mouthpieces of sensible size, the pressures which he gives should be corrected by $1{\cdot}505\,\frac{v^2}{2g}$.

This correction was made, and it was then found that with all the smaller tubes POISEUILLE's law held throughout his experiments, and with the larger pipe it held up to the critical value and then diverged in exact accordance with my formula, as shown by the line CC.

DARCY's experiments in the case of three tubes F, G, I fall below the critical value, and in all these cases agree very well with the theoretical curve as regards both branches.

This, however, must be looked upon as accidental, as at the lower velocities DARCY had clearly reached the limit of sensitiveness of his pressure gauges; thus, for instance, the experiment close by the letter F is the mean of two readings which are respectively 7 and 15; there is a tendency throughout the entire experiments to irregularity in the lower readings which may be attributed to the same cause, and this seems to explain the somewhat common deviation of the one or two lower experiments from the line given by the middle dots.

A somewhat similar cause will explain cases of deviation in the one or two upper experiments, for the discrepancy in the two gauges here again becomes considerable.

For these reasons the intermediate experiments were chiefly considered in determining the slopes of the theoretical lines.

These slopes were obtained as the mean of each class of tubes :—

Lead jointed	1·79
Varnished	1·82
Glass	1·79
New cast iron	1·88
Incrusted pipe	2·
Cleaned pipe	1·91

and then in the cases in which the temperature was given, I, J, L, M, N, the points O having being determined by the formula,

$$\text{Log } i_0 = 2 \log P - 3 \log D - 7{\cdot}851$$
$$\text{Log } v_0 = \log P - \log D - 2{\cdot}598$$

the lines having the respective slopes were drawn through these points and in all cases agreed closely with the experiments.

In the cases where the temperature was not given the values of log i_0 and log v_0 were calculated for 5° C., these are shown along the line marked "line of intersections at 5°," through these points lines are shown drawn at an inclination of 2 to 1, which are the lines on which O would lie whatever might be the temperature. These with the respective slope lines were drawn so as most nearly to agree with the experiments, these intersect the lines at 2 to 1 in the points O which indicate the temperatures, and considering the extremely small effect of the temperature these are all very probable temperatures with the exception of G, H, and S, in which cases O is above the line for 5° C. This indicates strongly that in these cases there must have been a small error, 2 or 3 per cent., in determining the effective diameter of the pipes.

It seemed very probable that roughness in the pipes, such as might arise from incrustation or badly formed joints, would affect the logarithmic homologues, and for this reason only the smoother classes of pipes were treated; but with a view to test this idea, the homologues Q and R, which related to the same incrusted pipe before and after being cleaned were drawn, and their agreement is such as to show that for such pipe the effect of incrustation is confined to the effect on the diameter of the pipe, and on the value of n which it raises to 2. This, however, was a large pipe and the velocities a long way above the critical velocity, so that it is quite possible that the same incrustation in a smaller pipe would have produced a somewhat different effect.

The general result of this diagram is to show that throughout the entire range—from pipes of 0·″000014 to 0·″5 in diameter, and from slopes of pressure ranging from 1 to 700,000—there is not a difference of more than 10 per cent. in the experimental and calculated velocities, and with very few exceptions the agreement is within 2 or 3 per cent., and it does not appear that there is any systematic deviation whatever.

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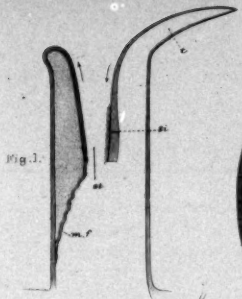

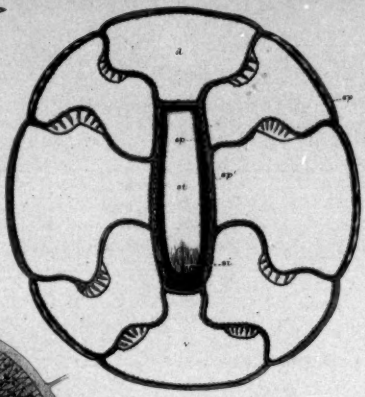

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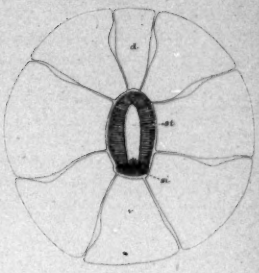

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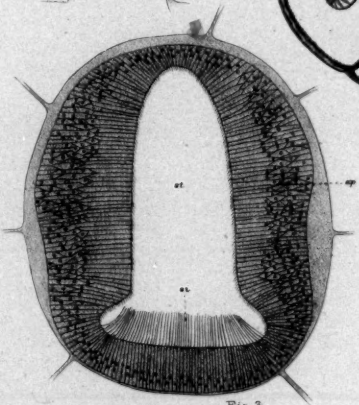

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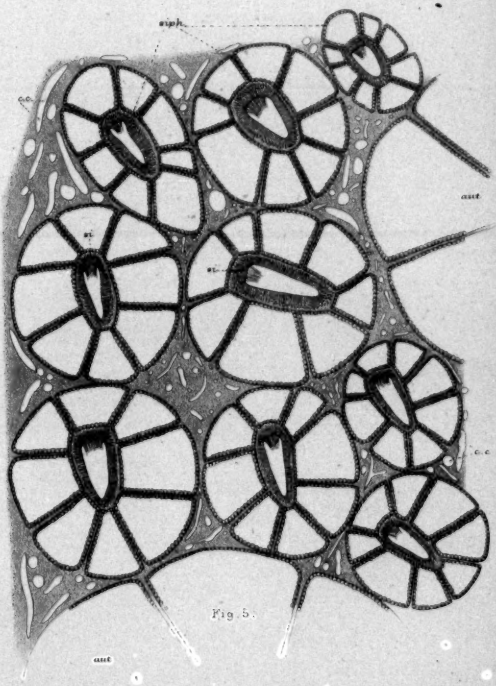

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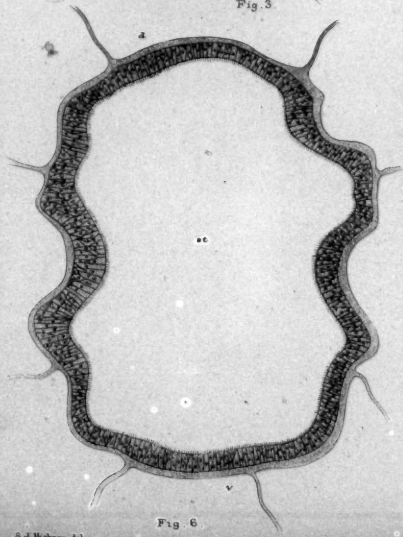
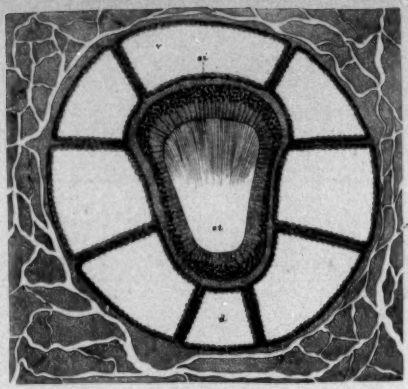


Fig. 6.

S. J. Hickson del.
W.H. Wesley lith.
West, Newman & Co. imp.



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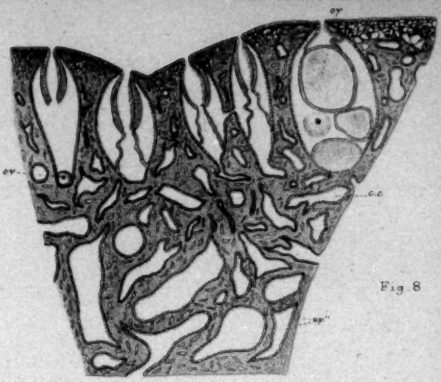

Fig. 8

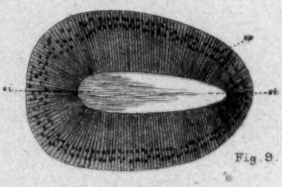

Fig. 9.

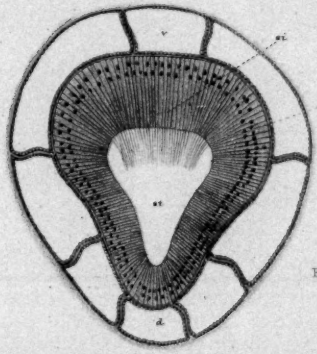

Fig. 10

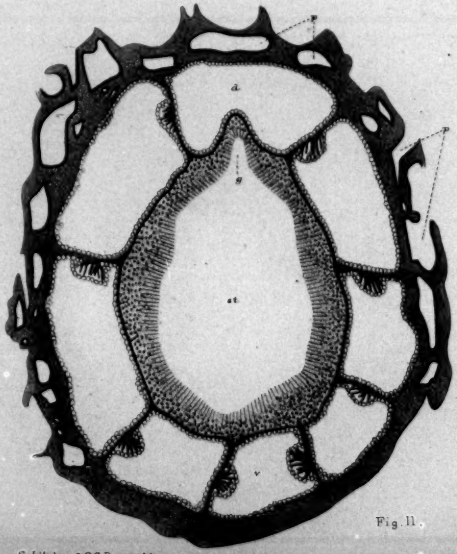

Fig. 11.

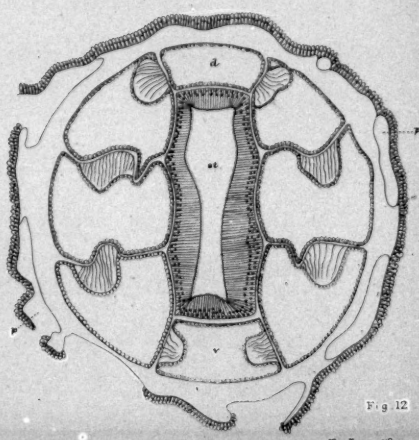

Fig. 12

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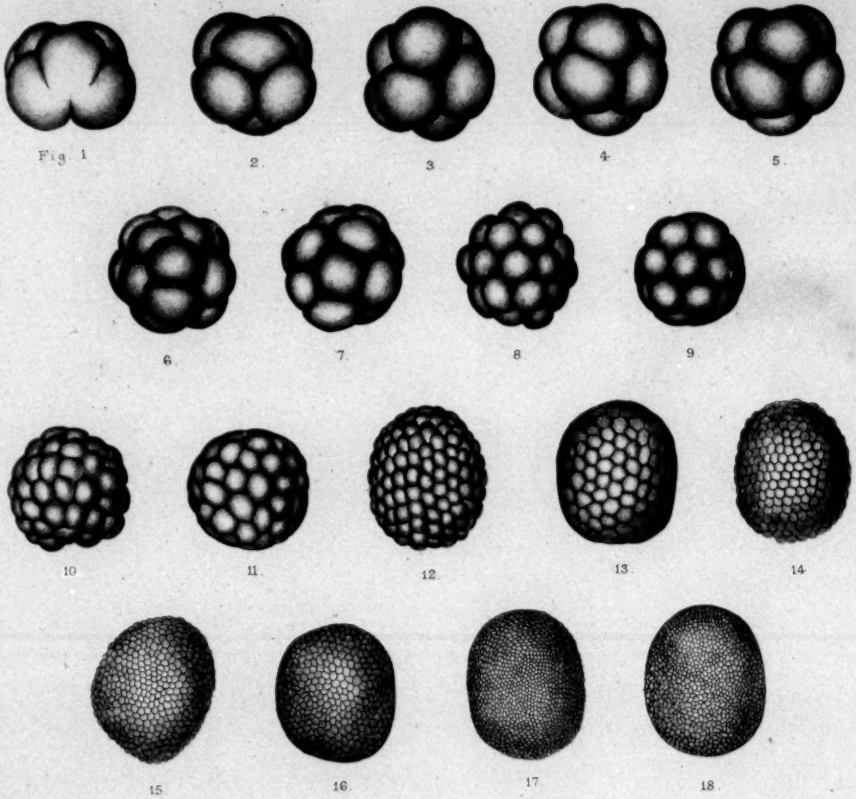

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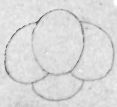
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West Newman & Co. lith.

Fig. 68.

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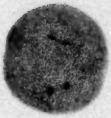

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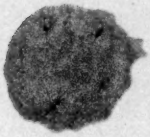

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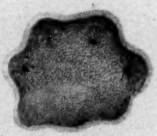

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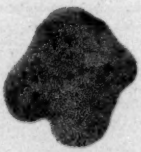

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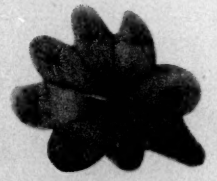

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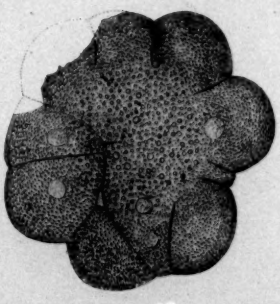

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West, Newman & C.t lith.

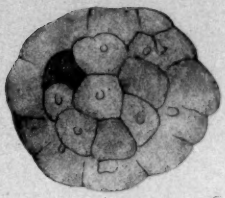
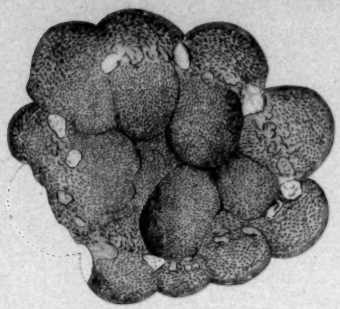


Fig. 97



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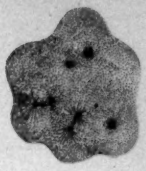

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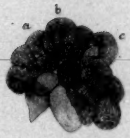

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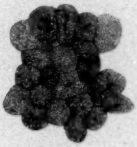

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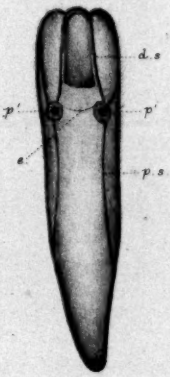

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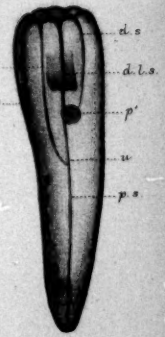

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Fig. 110.

Fig. 111.

Fig. 112.

Fig. 113.

Fig. 114.

Fig. 115.

Fig. 117.

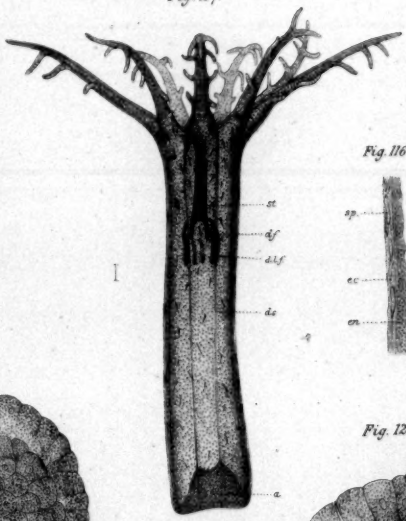
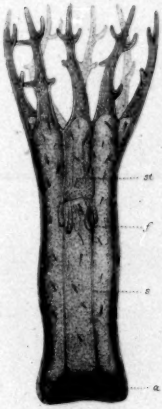


Fig. 116 a.

Fig. 116.



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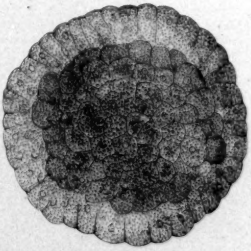

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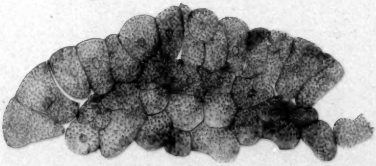

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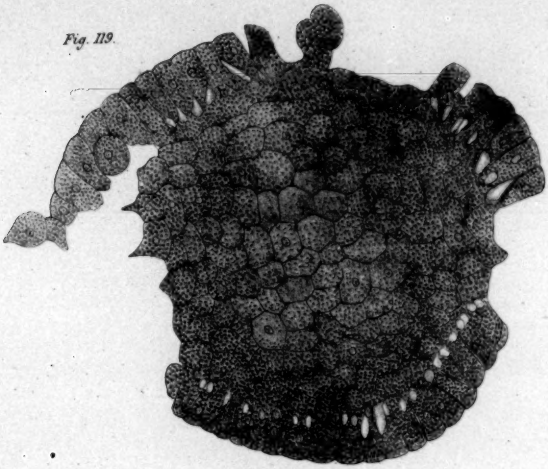
Fig. 119.



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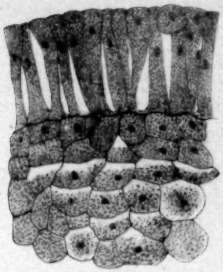

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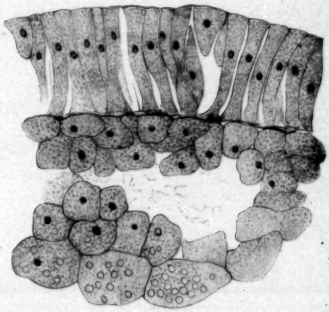

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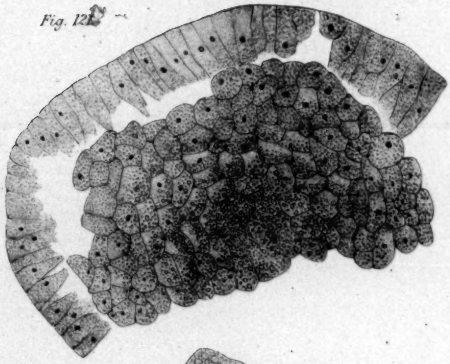

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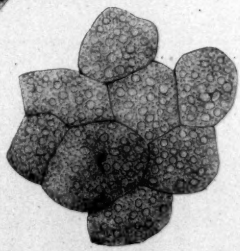

Fig. 125.

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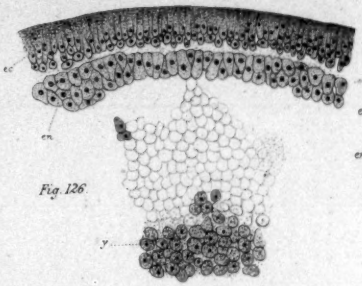
Fig. 126.



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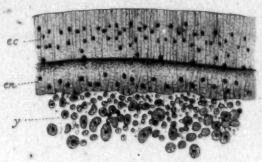

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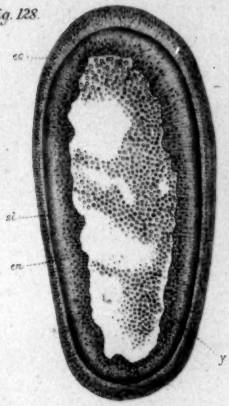

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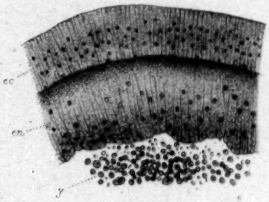

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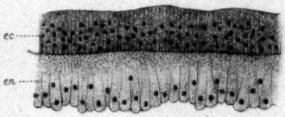
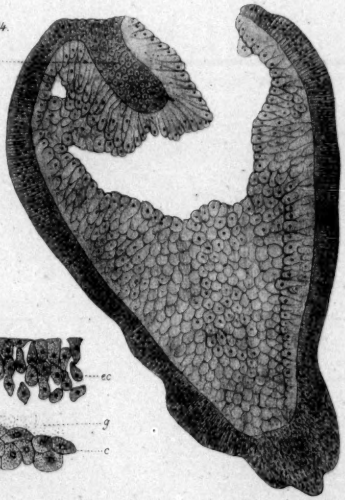


Fig. 132.

Fig. 134.



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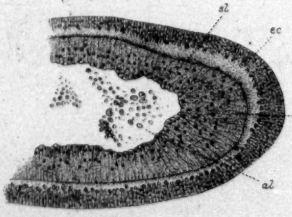

Fig. 131.

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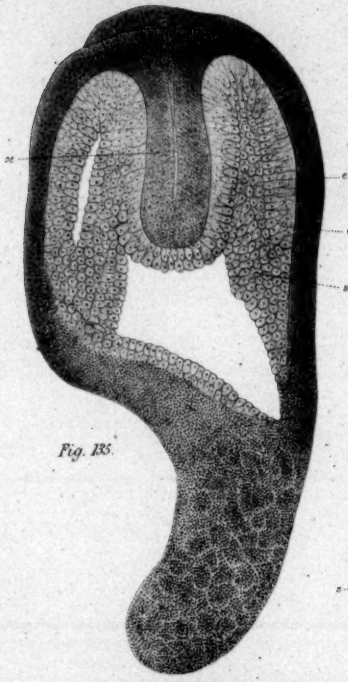

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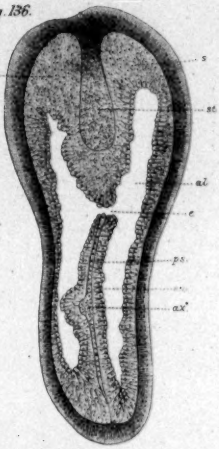
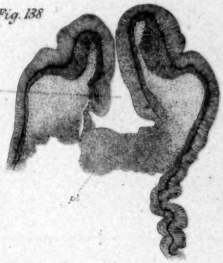


Fig. 136.

Fig. 137.



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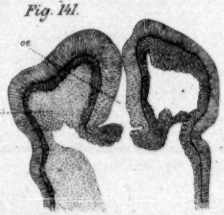

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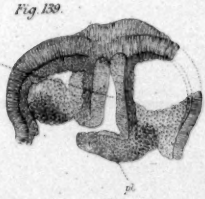

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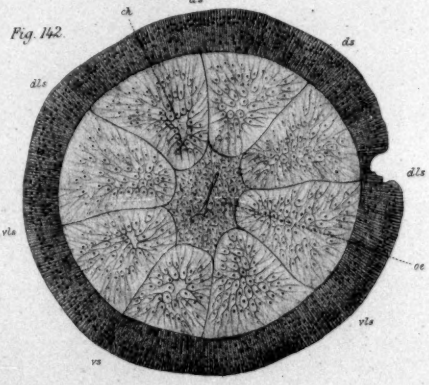

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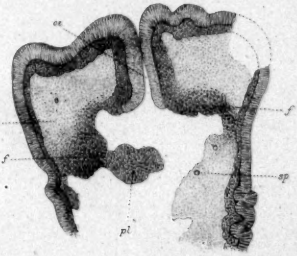

Fig. 140.

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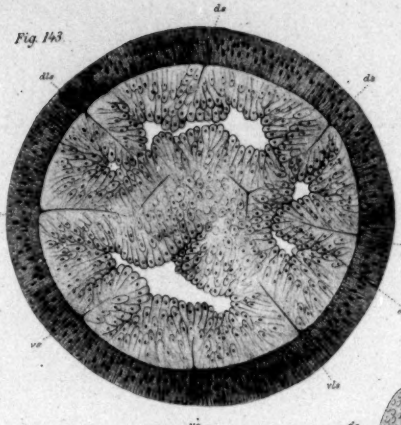
Fig. 143.



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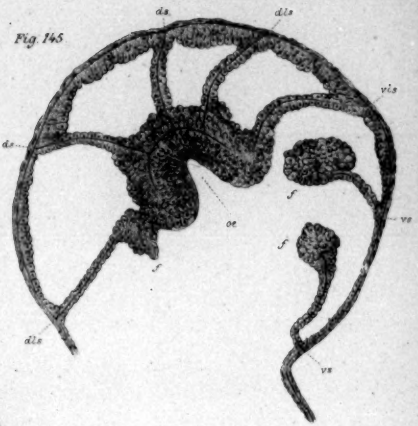

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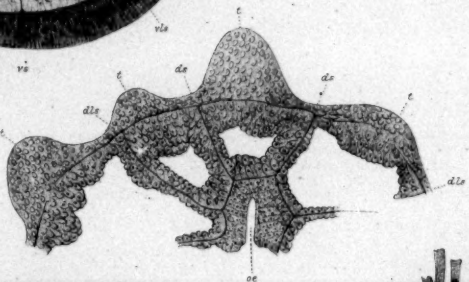

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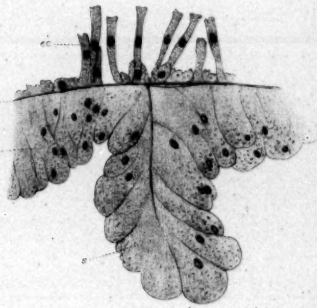

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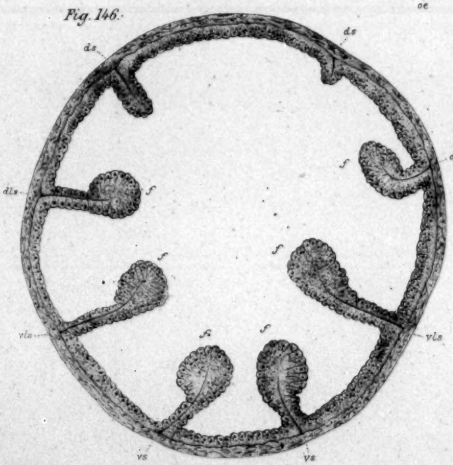

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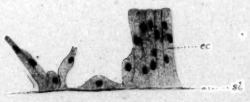


T. Huth, Lith^r Edin^r

Fig. 148.

Fig. 149.

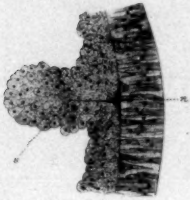
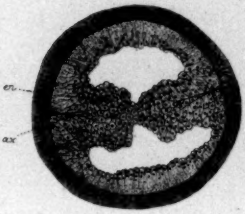


Fig. 150.

Fig. 152.



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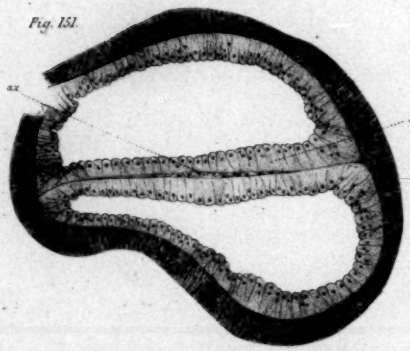
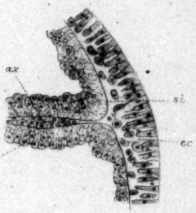


Fig. 153.

Fig. 156.



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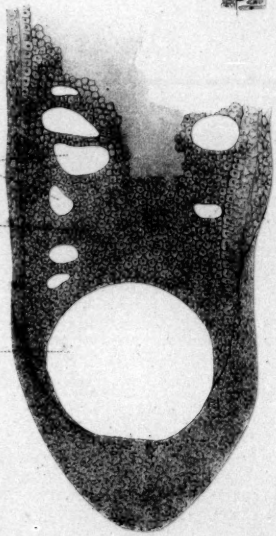
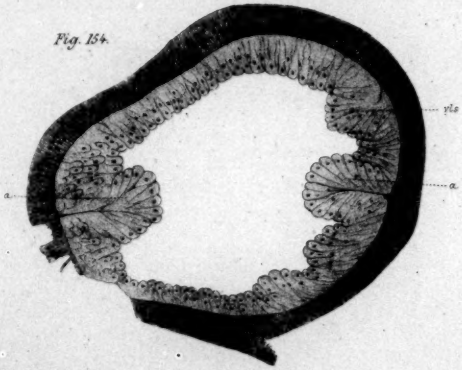


Fig. 154.



F Huth, Lith.t Edin.t

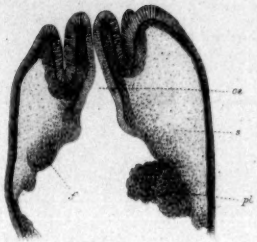
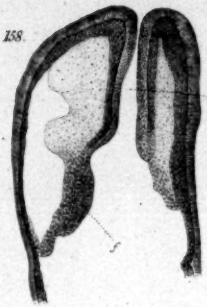


Fig. 157.

Fig. 158.



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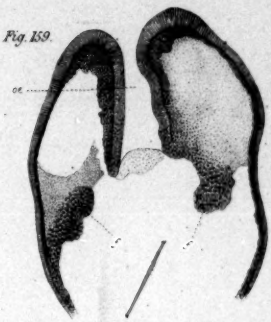

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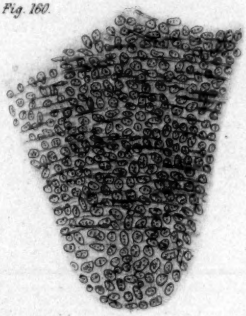

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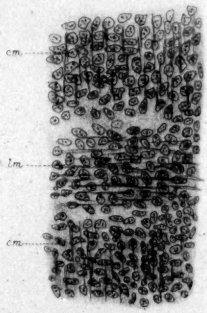

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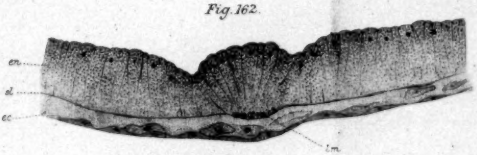

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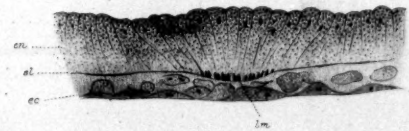

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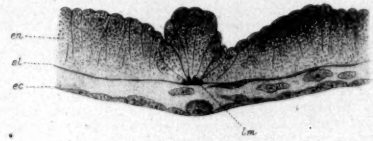

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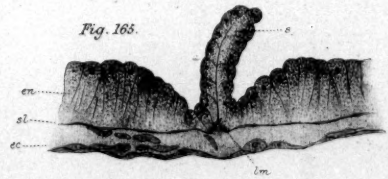
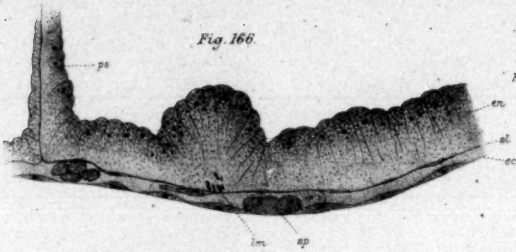


F. Huth, Lith^r Edin^r

Fig. 166.



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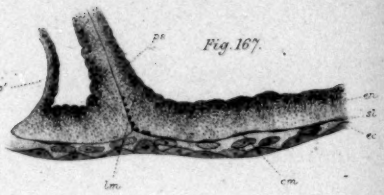
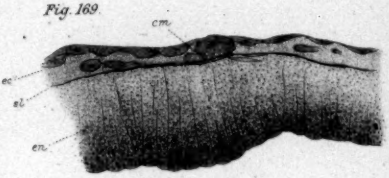


Fig. 168.

Fig. 169.



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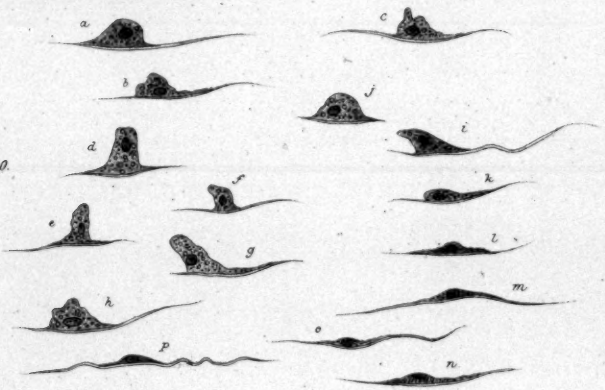
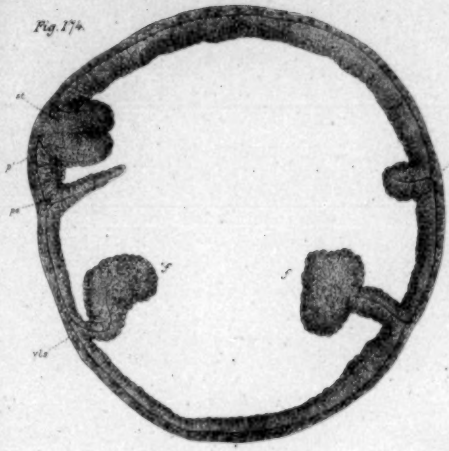


Fig. 171.

Fig. 172.

F. Huth, Lith.r Edin.r

Fig. 174.



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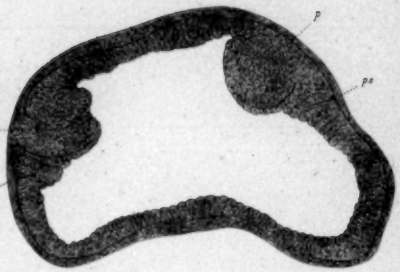

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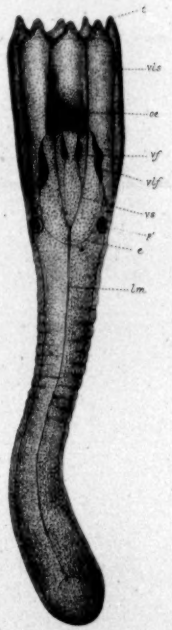

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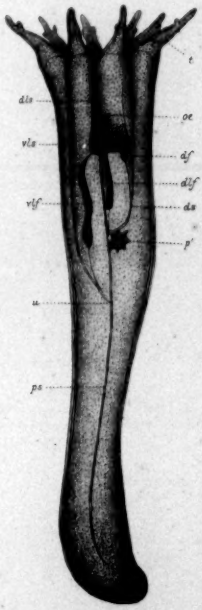

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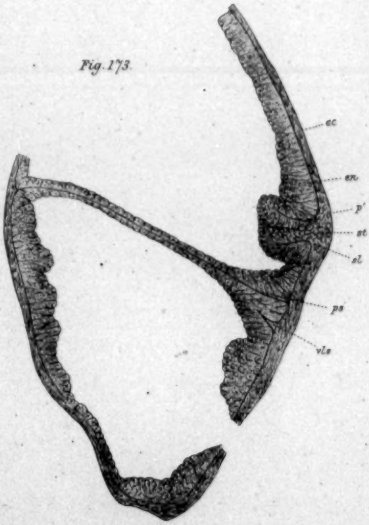
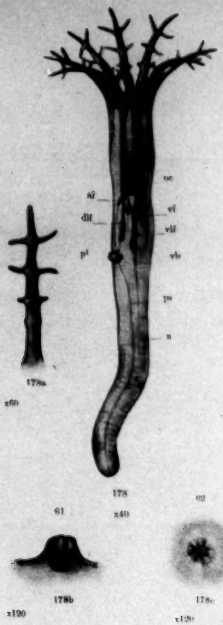
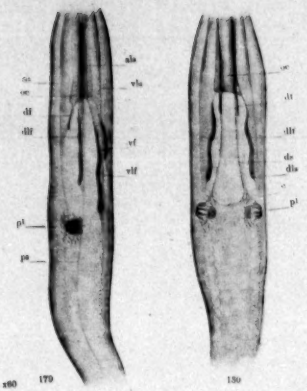
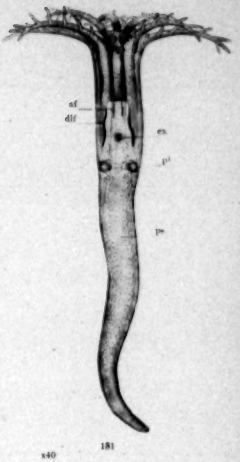
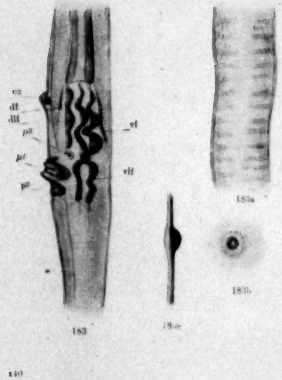


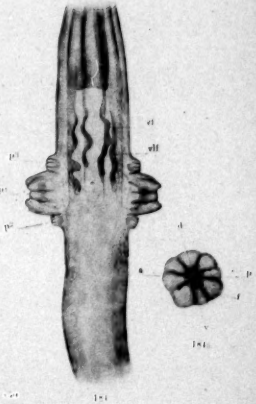
F. Huth, Lith^r Edin^r











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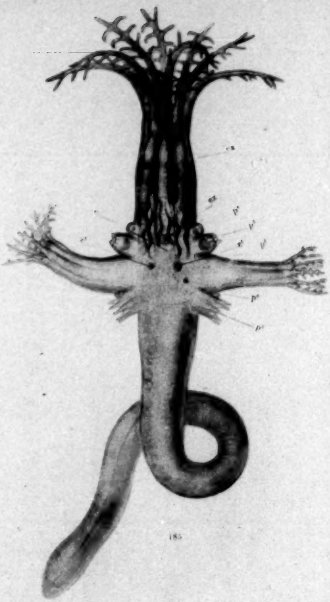

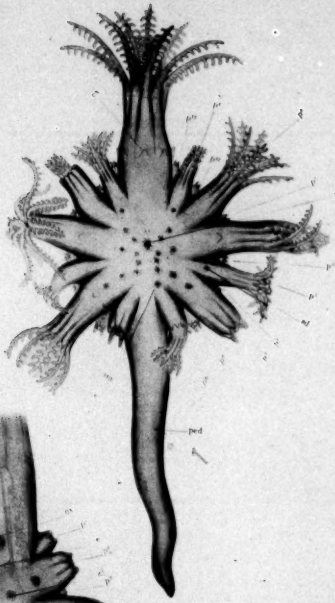

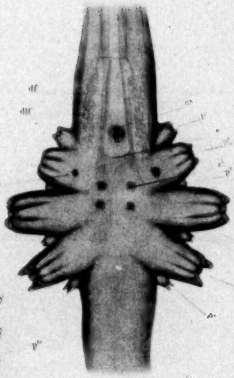

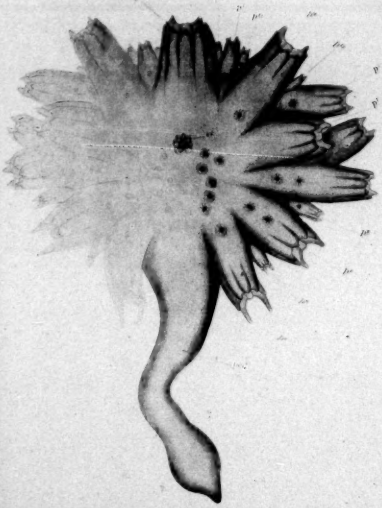

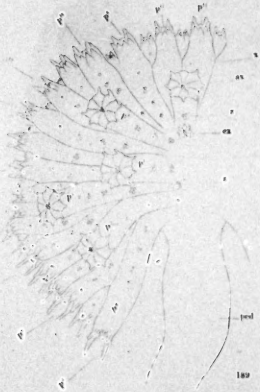

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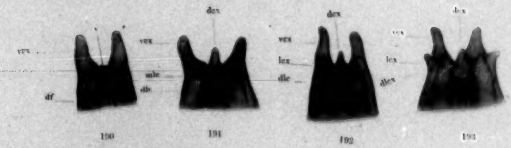

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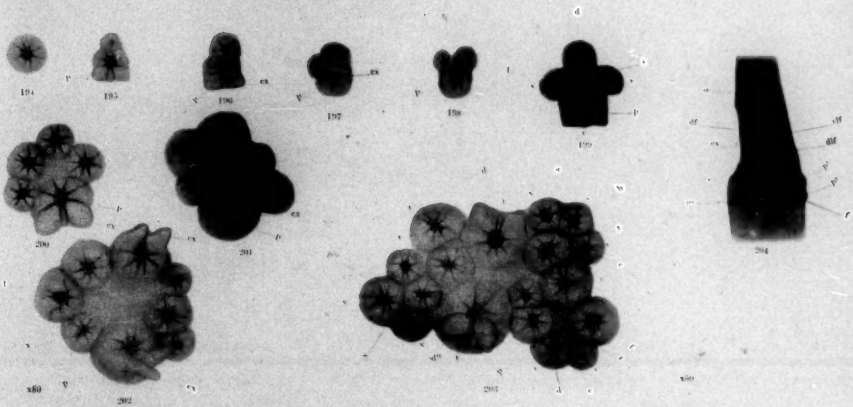

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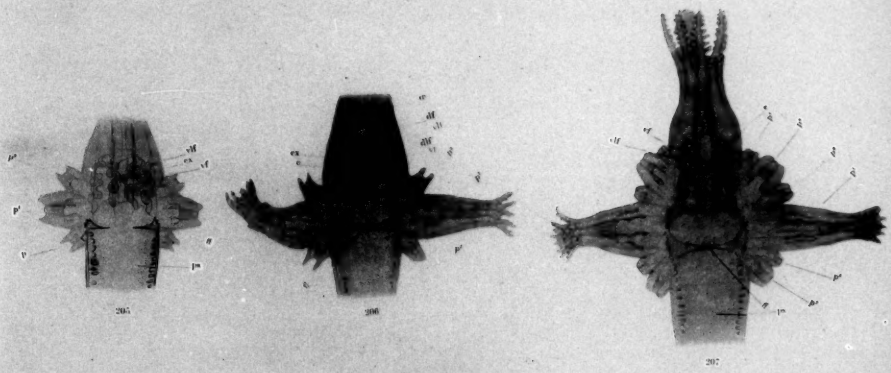


x50 x50

Photographed and Printed by the Photo-Electrotype Printing Company to Longmans from Tottenham

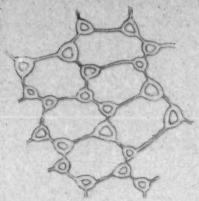


Fig. 4

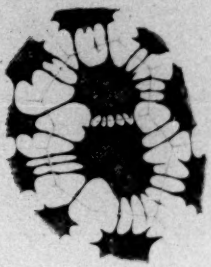
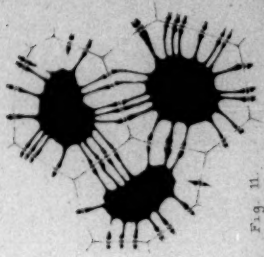


Fig. 7



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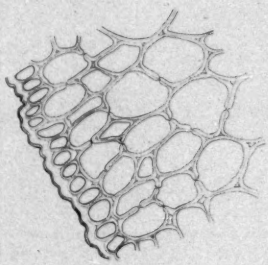
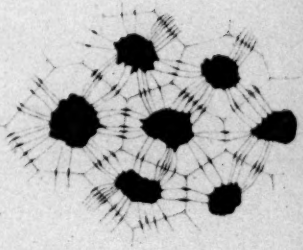


Fig. 3.

Fig. 8



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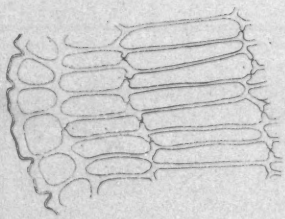

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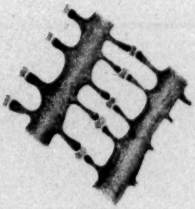

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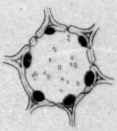


Fig. 12.

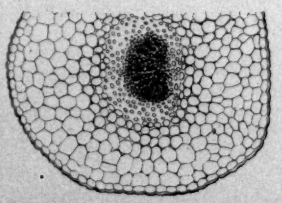


Fig. 1.

Fig. 5.

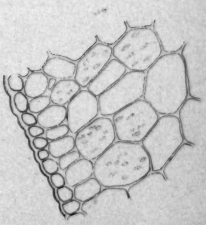


Fig. 9

W. Gardiner del.

West, Newman & Co. lith.

Fig. 13

Fig. 14

Fig. 15

Fig. 16

Fig. 17

Fig. 18

Fig. 19

Fig. 20

Fig. 21

Fig. 22

Fig. 23

Fig. 24

Fig. 25

W. Gardiner del.

West, Newman & Co. lith.

Fig. 28.

Fig. 35.

Fig. 36.

Fig. 40.

Fig. 29.

Fig. 32.

Fig. 34.

Fig. 39.

Fig. 27.

Fig. 31.

Fig. 33.

Fig. 38.

Fig. 26.

Fig. 30.

Fig. 37.

W. Gardiner del.

West, Newman & Co. lith.

Fig. 1.

Fig. 6.

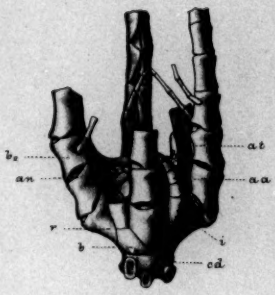


Fig. 2.

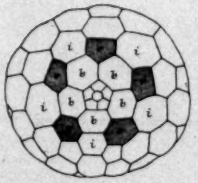
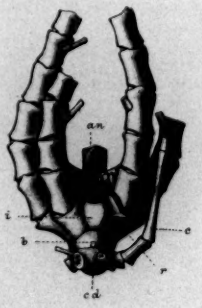


Fig. 7.

Fig. 8.



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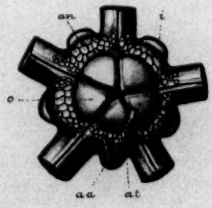


Fig. 5.

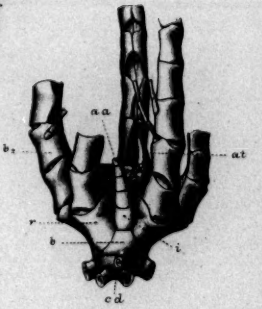


Fig. 4.

Barjeau & Highley del. et lith.

West, Newman & Co. lith.

THAUMATOCRINUS RENOVATUS, Nov. gen. et sp.

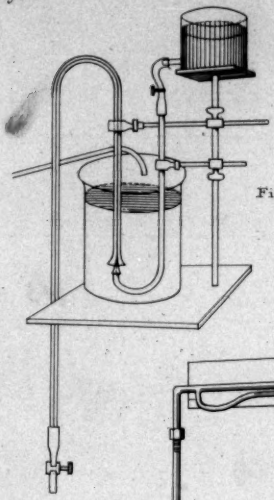


Fig. 10.

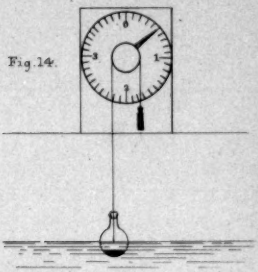


Fig. 14.

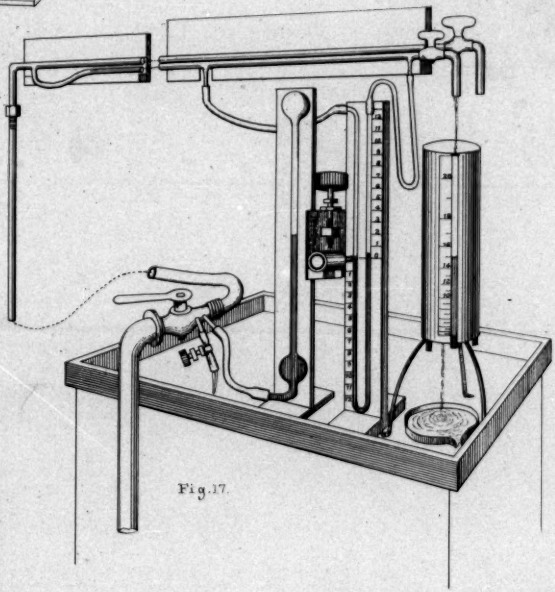


Fig. 17.

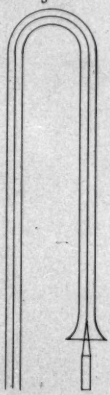


Fig. 10'

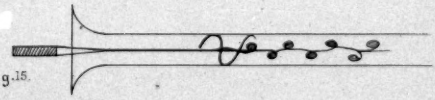


Fig. 15.

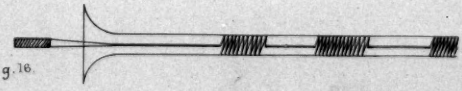


Fig. 16.

West, Newman & Co. lith.

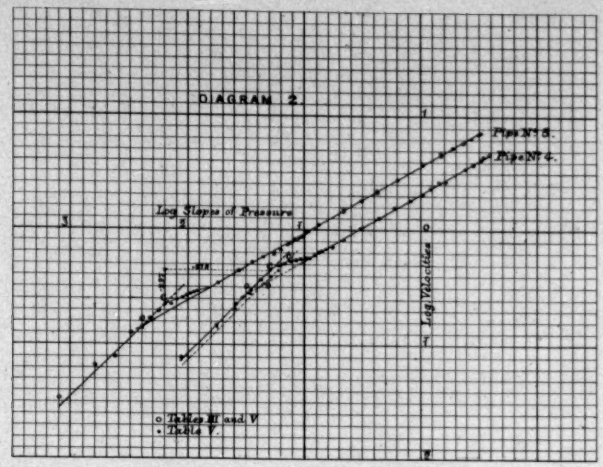


Fig. 11.

Fig. 13.

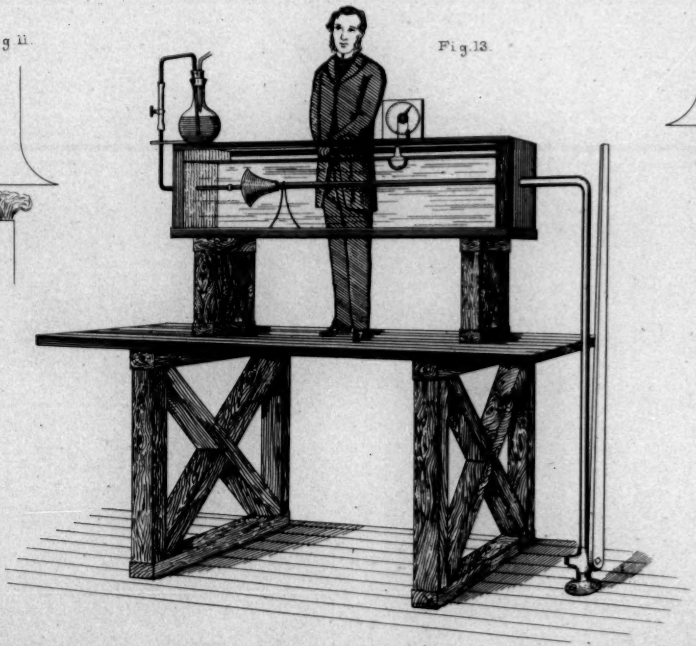
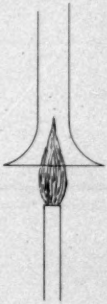


Fig. 12.



West Newman & Co. lith.

DIAGRAM I.

Curves of Pressure and Velocity in Pipes
N° 4. Diameter 0m·00515 at 5°c. and
N° 5. Diameter 0m·012,7

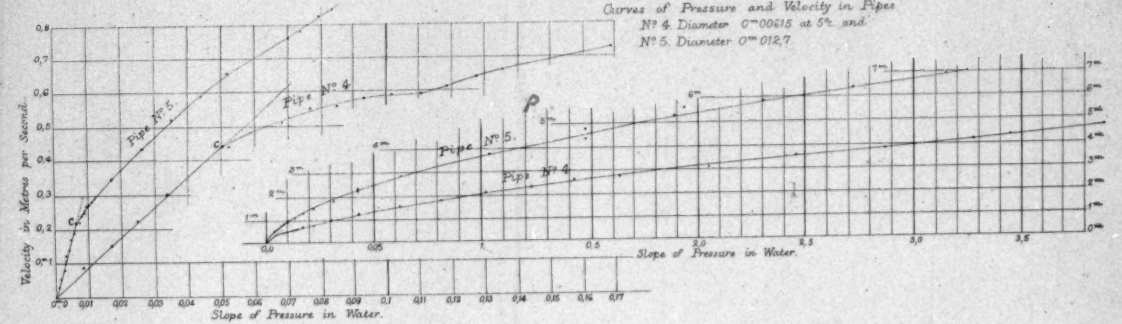
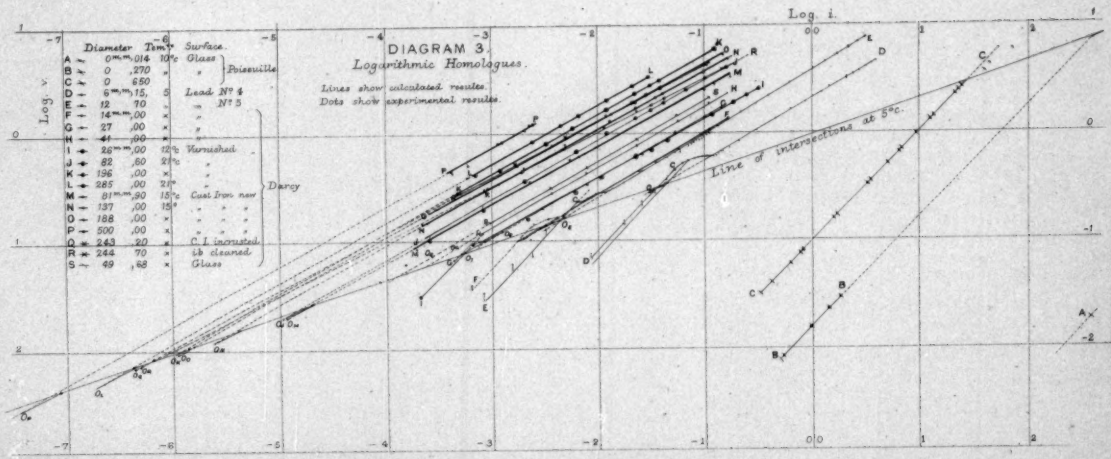


DIAGRAM 3.

Logarithmic Homologues.

Lines show calculated results.
Dots show experimental results.



		Diameter	Tem.°		
A	/	0m·m·,014	10°c	Surface.	Glass
B	/	0 ,270	"	"	" } Poiseuille
C	/	0 ,650	"	"	"
D	+	6m·m·,15	5	Lead. N° 4	
E	+	12 ,70	"	"	N° 5
F	+	14m·m·,00	×	"	"
G	+	27 ,00	×	"	"
H	+	41 ,00	×	"	"
I	+	26m·m·,00	12°c	Varnished.	
J	+	82 ,60	21°c	"	
K	+	196 ,00	×	"	
L	+	285 ,00	21°	"	
M	+	91m·m·,90	15°c	Cast Iron. new	} Darcy
N	+	137 ,00	15°	" " "	
O	+	188 ,00	×	" " "	
P	+	500 ,00	×	" " "	
Q	×	243 ,20	×	C.I incrusted.	
R	+	244 ,70	×	ib cleaned.	
S	+	49 ,68	×	Glass	

Phil. Trans. 1883. Plate 74.

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